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TRANSLATIONS

OF

FOREIGN BIOLOGICAL MEMOIRS

BURDON-SANDERSON

London
HENRY FROWDE

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TRANSLATIONS

OF

FOREIGN BIOLOGICAL MEMOIRS

I.

MEMOIRS

ON THE

PHYSIOLOGY OF NERVE, OF MUSCLE

AND OF THE

ELECTRICAL ORGAN

EDITED BY

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Oxford

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PREFACE.

THE following pages are intended to give the reader such preliminary hints as to the subjects of the Memoirs which are included in the present series of translations, as may aid him in using the volume either for the purpose of extending his knowledge of the branch of physiology to which they relate, or of obtaining information on special questions. It will be seen by glancing at the Table of Contents, that the Memoirs refer to three principal subjects, and that with one exception, that of Prof. du Bois-Reymond's research on Malapterurus, all have appeared within the last five years.

The purpose of the investigation recorded in the first Paper is to obtain a new proof of the well-known law established by Pflüger in his classical research on Electrotonus, published in 1859, relating to the changes of excitability of a nerve produced by the flow along it of a voltaic current. In 1881 the Author invented and described a new instrument, by which it is possible to subject a nerve to instantaneous mechanical excitation, of which the intensity can be measured and varied at will. When this is accomplished by the falling on the nerve of a weighted lever, it is found that the nerve is so little damaged thereby, that the excitation may be repeated as often as necessary without impairment of the effect, and that its strength may be graduated by the observer with an exactitude scarcely inferior to that which is attainable in the use of induction currents. As a means of measuring the excitability of a nerve, mechanical excitation has this great advantage as compared with excitation by induction currents, that it is free from those 'after-effects' of which the nature is so fully studied in the series of researches contained in Part II

of this volume; and secondly, that by the mechanical method it is possible to explore the condition of the nerve in the 'intra-polar' region, i.e. in that part of its course which lies between the inflow and outflow of the current. It may be stated generally that the observations of Tigerstedt made by so different a method, while they extend those of Pflüger, afford additional evidence of their accuracy, the only difference between them being that the state of diminished excitability at the cathode after opening of the current is found not to be so marked when tested mechanically as when tested electrically.

The second paper contains the results of a new investigation of the 'Law of Contraction,' with special reference to the conditions which determine the state of excitation that occurs at the anode at the moment that a current led through a motor nerve is broken. The author shows that these conditions correspond with those which produce ordinary negative polarisation in the nerve, that is, a state of the nerve in which, if the seat of outflow of the current be investigated immediately after the circuit is broken, it is found to be negative to all other parts; and he thinks that this correspondence is so close, that the two concomitant phenomena, viz. the contraction of the muscle and the polarisation of its nerve, must have the same cause. He is thus led to regard the make and break contractions as phenomena which are alike produced by the closing of a current, but which differ from each other as regards the way in which this current itself originates. This research should be read along with that of Grützner (No. 4) on the same subject, who by different experimental methods has arrived at the same explanation of the anodic contraction. He finds that by far the greater number of the known instances in which the phenomenon can be experimentally investigated admit of more complete and satisfactory explanation as resulting from negative polarisation than on Pflüger's theory. The special cases which he has investigated are—(1) that in which the anodic excitation produced by breaking a current which is led through a nerve in a direction opposed to the nerve-current, is found to be dependent on certain complicated but

well-ascertained relations between the strength of the former and that of the latter (see Introduction to Grützner's paper); and (2) the numerous cases in which excitation at the anode results, not from break of the current, but from sudden diminution of its strength. In these the varieties of effect which are observed are, in Grützner's opinion, such as point to polarisation, not subsidence of anelectrotonus. How far this way of looking at the subject is justified, the reader will be able to judge after studying the criticisms of Prof. Hermann and Prof. du Bois-Reymond.

In No. 5, Prof. Hering has investigated the excitation of motor nerves by voltaic currents from an entirely different point of view. More than thirty years ago du Bois-Reymond showed by a remarkable experiment (see p. 128), in which he used no apparatus excepting 'physiological clay,' that is, clay kneaded with 'normal' salt solution instead of water, that if the cut and natural surfaces of a nerve-muscle preparation are bridged, the muscle contracts when the bridge is completed, and again when it is broken. Starting from this observation, the author proceeds to illustrate, by a variety of new modes of experiment, the exciting influence exercised on nerve by its own current. He shows, for example, that the mere falling of the end of a nerve on a moist conductor (p. 130) produces contraction when the contact is of such a nature as to bridge the two surfaces, that by this means, if the contact is repeatedly made and broken, a tetanus 'without metals' may be produced, and that a real 'secondary twitch from nerve' is obtainable when one of two nerves is excited, of which the two ends are applied to each other with their cut surfaces in the same plane and looking in the same direction. When this is the case, the muscle to which the unexcited nerve belongs responds to excitations of a distant part of the other by currents of minimal intensity. In this respect the phenomenon may be contrasted with du Bois' 'paradoxical twitch,' which, as is well known, only appears when the exciting currents are strong, and led in in pretty close proximity to the contact between the two nerves. He finally shows how the effects of opening and

closing of external currents are modified by the excitatory influence of the nerve-current, and how impossible it is to judge of or interpret these effects correctly without taking this 'interference' into account. It is to be noted that Prof. Hering is led by his observations to a conclusion as to the nature of the opening contraction, which, although by no means identical with that arrived at by Tigerstedt and Grützner, is in intelligible relation with it.

The second Part begins with three independent investigations of the same subject by three of the most distinguished living physiologists—the first by Prof. du Bois-Reymond, of Berlin; the second by Prof Hering, of Prague; the other by Prof. Hermann, of Zürich, now of Königsberg—all of which were published within a few months of each other. The purpose of du Bois' paper is to give a more full account, based on new experimental investigations, of the phenomena which the author discovered many years before and designated by the term 'positive polarisation.' In muscle and nerve there are, according to him, two kinds of polarisation, of which one is identical with physical polarisation of porous bodies steeped with electrolytes, the other is purely physiological, that is, peculiar to living excitable structures. As it manifests itself in muscle and nerve, positive polarisation consists in this, that when either of these structures is traversed axially by a voltaic current of very short duration, the galvanoscopical after-effect observed on opening, instead of being, as in ordinary polarisation, opposed in direction to the led-in current, is in the same direction with it, varying according to the density of the external current and other well-defined conditions which need not here be referred to, but exhibiting throughout the most intimate association with the functional activity of the organ.

A few months later in the year in which du Bois presented his Memoir to the Berlin Academy, a communication on the same subject was submitted to the Academy of Vienna by Hering, in which he described the same phenomena under another designation, the main fact being that when a current

of considerable intensity and short duration is led through a muscle, and the condition of the muscle is immediately after investigated galvanoscopically, it is found that a sudden change as regards its electrical condition takes place, of such a kind that the current led off from the organ, at first feebly 'negative,' that is, in the opposite direction to that of the external current, becomes strongly 'positive,' that is, in the same direction.

Similarly, Prof. Hermann, in a Paper published in Pflüger's Archiv in January 1883, gave an account of the same phenomena, which, as regards muscle, closely accorded with that of Hering, adding new proof of the polar localisation of the electromotive changes observed; and he further extended his researches from muscle to nerve so as to include all the subjects investigated by du Bois, with the exception of that of the electrical organs of fish. Prof. Hering's paper ('Ueber Veränderungen des electromotorischen Verhalten der Muskeln in Folge electrischer Reizung') we have not thought it necessary to translate, preferring to present to the reader the more advanced view of the subject contained in his second paper, which appeared at the same time with it, under the title, 'Ueber du Bois-Reymond's Untersuchungen der secundärelectromotorischen Erscheinungen am Muskel.' The reader will find in the three papers satisfactory evidence that all these distinguished observers have had before them the same facts, though from difference of method, or from other causes, they may have been presented to them under different aspects. But in all that belongs to the doctrine of 'secondary electromotive phenomena' it will be equally clear to him, that while Hering and Hermann tend in the same direction, their views are utterly at variance with those of the great founder of Electro-physiology.

Du Bois holds that just as in the ordinary polarisation of porous bodies soaked with electrolytic liquids, the change affects all parts through which branches of current pass, so in polarisation of nerve and muscle, whether negative or positive, the change affects all the parts traversed in a degree which depends upon the current density, and that as regards positive polarisa-

tion, the action of the current is directly exerted on certain hypothetical carriers (Träger) of electromotive forces which are distributed throughout the polarisable structure, and which the current is capable of 'directing' (see concluding paragraph of No. 6).

Hering rejects this theory on the ground that the changes of which 'positive polarisation' is the expression, have their seat exclusively at the anode, and explains the experimental facts used by du Bois in proof of 'internal polarisation' (that is of a polarisation affecting all traversed structures, and consisting in the coming into existence of electromotive forces all along the line of flow, and not merely at anodes or cathodes), on the supposition that he employs structures in which, in consequence of their heterogeneity, such sudden transitions from less to greater density occur in the course of the current-paths, that the effects of anodes are produced. On the assumption that positive polarisation has its seat at the anode exclusively, he has no difficulty in referring what is observed to the well-recognised facts—(1) that the effect of opening a current led through a muscle or nerve is to produce excitation at the anode; and (2) that the characteristic expression of the excitatory state is negativity; and accordingly, while recognising the essential relation of the change in question to the functional activity of the organ in which it manifests itself, he prefers to speak of it as 'anodic after-effect' rather than as 'positive polarisation.'

Hermann objects to the term 'positive polarisation' even more decidedly than Hering, on the ground that the phenomenon is not analogous to physical polarisation. He, like Hering, believes it to be excitatory, and holds that it is due to the setting up of a persistent change of this nature in the neighbourhood of the spot at which the current has entered. Among the various experiments which lead to this conclusion, those are of most importance which show (1) that in muscle it is confined to the anodic region; (2) that it is annulled whenever the current is led into the muscle or nerve through a dead part; and (3) that the anode becomes relatively negative not only

to the 'intra-polar' region, but also to extra-polar parts in its neighbourhood. Hermann is accordingly led to regard all secondary electromotive phenomena as resulting from the interference of the excitatory change which occurs at the anode in consequence of the opening of the current, with ordinary galvanic polarisation, it being understood that the physical change always anticipates the vital one as regards the order of its occurrence; so that whenever the conditions (strong current and short closure) are such as to enable these two antagonistic influences to manifest themselves together, the process consists of a more transitory physical effect, which is followed by a more lasting physiological one.

If the views of Hermann and Hering are accepted, the reader will see that the form given by Tigerstedt and Grützner to their theory as to the essential nature of the opening contraction must be modified. Tigerstedt assumes that at the break of a current, the anode becomes, in consequence of negative polarisation, virtually a cathode, an assumption which takes no account of the facts of positive polarisation. On this point the reader will compare with advantage du Bois' criticism of Tigerstedt in his sixteenth paragraph, with that of Hermann in the paragraph which precedes his conclusion.

If it is true that 'positive polarisation' of a nerve or of a muscle is in reality a purely physiological, or, in other words, an excitatory effect of the leading through it of a voltaic current, it becomes of interest to enquire what is the relation of the electrical after-effects so fully studied by du Bois-Reymond, Hering, and Hermann, to the more mechanical effects which form the subject of the first part of this series. In general it is, as every physiologist knows, extremely difficult to demonstrate in detail the correlation which undoubtedly exists between the electrotonus of Pflüger, and the galvanoscopic phenomena which were originally investigated by du Bois and treated of by him under the same title. The chief reason of the difficulty lies in the circumstance that until recently it has been possible to investigate the former only in muscle, the latter only in nerve. But

from the moment that it was shown by Hermann and Hering's researches, that the well-known electromotive after-effects of the current in nerve (du Bois' electrotonus) have their counterparts in muscle, that is, that the electrical state of a muscle which is traversed axially by a current is subject to polar variations which correspond to an- and cathelectrotonus, it at once became of interest to enquire how these variations are linked to concomitant changes in what must always be regarded as the essential function of muscle—that of contracting in response to stimulation.

In 1881 it was discovered by Engelmann that the anodic and cathodic localisation of the closing and opening excitatory effects could be demonstrated in the heart of the frog, and Hering showed how, with the aid of the double myograph, as much could be done with a striated muscle. Electrotonus of muscle was thus in a certain sense demonstrated, but to complete the proof it was necessary to show that as cathelectrotonus is represented by contraction, so anelectrotonus is represented by relaxation. This was accomplished by Prof. Biedermann, Hering's coadjutor at Prague, in 1883[1]. It was necessary for the purpose to employ as subject of experiment a muscular structure capable of persistent tonus, for it was only in such a structure that relaxation could be observed. The required condition was found to be fulfilled by the heart of the snail (Helix pomatia), which, as Biedermann discovered, can generally be thrown into spasm of sufficient duration for the purpose, by the simple expedient of allowing the ventricle to contract against unwonted resistance. By the observation that the closure of a battery-current through the heart leads to relaxation which takes its start from the anode, just as in the relaxed heart, the closing contraction takes its start from the cathode, Biedermann was able to prove that in that structure, relaxation of muscle already contracted is as characteristic of anelectrotonus, as contraction of relaxed muscle is of cathelectrotonus.

[1] W. Biedermann, Ueber das Herz von Helix pomatia. (Ein Beitrag zur vergleichenden Physiologie der Muskeln.) Wiener Sitzungsberichte, vol. lxxxix. 19–55.

In the paper of which a translation is introduced into our series of Memoirs, Biedermann extended the same mode of experiment to a striated muscle of the frog. In order to bring about a similar condition of permanent spasm to that which, in the heart of Helix, is produced so easily by mere distension, he availed himself of the action of veratrine, and found that in this, as in the other case, the cathodic contraction is replaced by anodic relaxation, and the anodic contraction by cathodic relaxation. Here, then, an opportunity seemed to be afforded for the first time, of determining experimentally whether electrical and functional electrotonus occur under the same conditions — whether, as the opening contraction corresponds with the anodic after-effect (of which, according to Hering, positive polarisation is but the expression), the cathodic break-relaxation is marked by a cathodic after-effect, which, although of opposite sign, i.e. positive, as regards the condition of the cathode itself, is of the same sign galvanoscopically. To ascertain whether it was so or not, Biedermann prepared the sartorius by subjecting one end of it to the action of veratrine, leaving the other intact, and then induced cathelectrotonus in the poisoned, that is, tonic end, leading a battery-current through the whole riband for a couple of seconds. The poisoned end was at once thrown into veratrine spasm and the cathode became negative; but when (after compensating) the current was again closed, its after-effect was in the opposite direction, that is, in the direction of the exciting current. In other words, relaxation of the veratrine spasm was, as was expected, accompanied by diminution of the negativity which is its galvanoscopic expression. When the same observation was made with the modifying current in the opposite direction, that is, with the anode at the veratrine end, it was similarly found that a current led through during spasm was reversed, that is, that the anode became positive.

The general conclusion derived by Biedermann from these experiments is that the state of muscle varies, not merely between the state of excitation and the normal, or unexcited

state (the former being indicated galvanoscopically by the presence in the tissue of a current from the excited to the unexcited part, and mechanically by the presence of more or less spasm, the latter by the opposite effects), but that muscle varies in the direction of greater or in that of less fitness for functional activity. By employing such terms as 'up' or 'down' to denote these two tendencies, it is possible to express his conception thus :—A voltaic current produces at the anode when it is closed an 'up' state, of which the galvanoscopic sign would be relatively positive, and the mechanical sign axial extension but aptness to contract; at the cathode a 'down' state, associated conversely with 'negativity,' and axial shortening. The assumption of a state intermediate between these two is suggested by the indications of what, for want of a better name, is called by Biedermann 'reaction,' that is, of a tendency (of which the behaviour of all excitable tissues suggests the existence) to assume a condition opposite to that in which it actually is, by virtue of which the 'down' state is produced at the anode at make, the 'up' state by the cathode at break. In Biedermann's experiments it was strikingly seen that the same external cause produces contraction and negativity when acting on muscle in the 'up' state, relaxation and positivity when acting on the same muscle in the 'down' state. This being so, there may be between contraction and complete relaxation an intermediate state in which the two opposite tendencies neutralise one another. If such a state exists, it does not follow that it is the normal state of the tissue, for by the word normal the physiologist understands simply the state which best fits the structure for its function, and cannot be guided in his use of it by the correlation of its elementary properties.

Part III contains Prof. du Bois-Reymond's investigations in a field of research in which up to the present moment he has been almost the only worker—that of the electrical phenomena of fish which are possessed of special electrical apparatus. The Memoir on Malapterurus, which appeared a few years ago in the Author's

Collected Papers, has been translated at his suggestion. It contains a full description of the methods by which the difficulties of the investigation were in the first instance overcome, and the reader will find it to be an indispensable introduction to the other two Memoirs on Torpedo, which contain his more recent observations. As each of the three memoirs is complete in itself, and is preceded by a summary of the subjects discussed in each paragraph, no introduction is needed. It may not, however, be out of place to draw attention to the very remarkable discoveries recorded in the concluding paper relating to the fact of 'irreciprocal conduction,' which the author has proved to exist in a remarkable degree in the columns of the electrical organs of Torpedo.

The Editor regrets that the publication of the volume has been unduly delayed, in consequence of the unexpected difficulties experienced by the translators in their work. The subject is so new to English scientific literature, that much time is unavoidably lost in deciding between the two alternatives, of using Germanised phraseology and of coining English equivalents for the forms of expression used by German writers. In general, the latter alternative has been preferred, but not without a heavy sense of responsibility. Whether successfully or not, great pains have been taken to select such equivalents as appear most accurately to express the meaning of the original, and the translators have, as a rule, consented to employ the same equivalents for the same words.

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CORRIGENDA.

P. 6, note 2, *for* fortschritte *read* Fortschritte.
P. 7, note 4, *for* nouvelles *read* nouvelle.
P. 23, § 2, *for* irritability *read* excitability.
P. 56, line 4 from top, *for* Marcy *read* Marey.
P. 56, Exp. II, heading, *for* . . . . *read* the break-contraction.
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P. 94, line 13 from bottom, *for* break *read* make.
P. 123, line 18, *for* Thermopyle *read* Thermopile.
P. 166, line 15, *for* through *read* in.
P. 168, line 19, *for* polarisation-current *read* effects.
P. 187, line 13 from bottom, *for* would *read* should.
P. 203, line 19 from bottom, *for* Sect. 2 *read* p. 163.
P. 204, line 13 from bottom, *for* that *read* of.
P. 204, line 11 from bottom, *for* Sect. 9 *read* Sect. 10.
P. 249, line 4, *for* Sect. 9 *read* Sect. 8.
P. 277, note 1, *for* p. 404 *read* p. 343.
P. 280, line 2 from bottom, *for* Sect. 1 *read* Sect. 21.
P. 297, line 11, *for* or *read* in the.
P. 343, note, *for* No. V *read* No. VI.
P. 471, line 3, *for* positive *read* negative.
P. 490, line 6 from bottom, *for* No. V *read* No. VI.
P. 504, note, *for* p. 224 *read* p. 457.

PART I.

RESEARCHES

RELATING TO THE

"LAW OF CONTRACTION."

I.

CHANGES OF EXCITABILITY

PRODUCED IN

NERVES BY A CONSTANT CURRENT.

By Dr. ROBERT TIGERSTEDT.

mmunicated to the Swedish Royal Academy of Sciences, April 12, 1882.

I.

In his famous investigations into the physiology of electrotonus, Pflüger, in the year 1859, submitted the changes of excitability in nerves elicited by a constant current of electricity to an experimental examination which will stand to all time as a model for similar investigations, as regards both the number and variety of the methods of research employed and the completeness of the experimental criticism. As test-stimulus he employed partly the constant current, partly the induction-shock, and in part also he used chemical stimuli. The most important actual relations established by this investigation are, very briefly, as follows. In the region of the positive pole of the current the excitability of the nerve is diminished, as well in the extrapolar as in the intrapolar direction; and the diminution attains its definite amount gradually, being not so great for some moments after the current is closed as it afterwards becomes. When the current is opened there occurs immediately an increased excitability, which may last for a longer or shorter period. In the region of the negative pole of the current the excitability of the nerve is increased as well in the extrapolar as in the intrapolar direction. This increase occurs directly after contact is made. When contact is broken, diminished excitability is exhibited if the current is weak or moderate, which, however, after an exceedingly brief interval gives place to a condition of increased excitability lasting a longer or shorter time.

It is at the poles that the change in excitability is greatest, diminishing as we leave these both in the extrapolar and intra-

polar directions. The greater the strength of the polarising current, the greater is the change of excitability and its extrapolar extension. Between the poles the diminution of excitability extends as the strength of the polarising current increases; or, to put it otherwise, with increasing strength of current, the indifference-point moves gradually from the positive to the negative pole.

The greater the separation of the electrodes the greater is the tract of nerve over which the extrapolar change of excitability extends. The behaviour of the intrapolar tract is absolutely the same whatever the distance between the electrodes.

To test the local changes of excitability in the intrapolar tract Pflüger used chemical stimuli; the induction-coil he employed only to investigate the total excitability. He abstained from examining the changes of excitability with sharply localised electrical stimuli fearing an escape of electricity between the constant and test currents.

An important, though perhaps not unexpected, addition was made to these results two years after their publication by Obernier in a research carried on under Pflüger's guidance. Obernier proved by experiments that, with the application of strong polarising currents (6–8 Groves), there occurs at the negative pole in the first moments after contact is broken a very considerable diminution of excitability[1].

Before this, however, attacks had been made on the correctness of Pflüger's results—attacks which have since been from time to time renewed by various enquirers. The most notable fact, however, is, that all those who have thus assailed Pflüger, with few exceptions, have conducted their counter-researches with nothing like the same care as Pflüger employed. What Meissner says of one of the first of them may be applied with justice to them all. 'Inasmuch as Pflüger has grounded all his enunciations on investigations made with every kind of efficient stimulus, one has a right to demand from a criticism which is directed to prove these enunciations in part untenable, that it be pursued on a like basis and with a similar use of every species of stimulus[2].

To this category of works we must refer those of Schiff[3], of

[1] Obernier, Archiv für Anatomie und Physiologie, 1861, pp. 268–278.

[2] Meissner, Bericht über die fortschritte der Anatomie und Physiologie, 1863. Leipzig, 1864, p. 359.

[3] Schiff, Lehrbuch der Nerven-physiologie, Jahr 1858–59, p. 94.

Budge[1], of Valentin[2], of Schiff and Herzen[3], and of Lautenbach[4]. Thus we have the employment of metallic instead of unpolarisable electrodes; no measures of precaution are mentioned as being used to prevent escape of current from one circuit into the other; experiments are carried out on one and the same nerve in such a way that the direction, as well of the polarising as of the test current, is many times reversed; and so on. Under such circumstances it was impossible to arrive at clear and unambiguous results. Schiff avows too '*that to bring together all tolerably similar results of experiment would seem to produce a perfect chaos*[5].'

Small as was the impression which the works I have mentioned were able to make on Pflüger's results, these were equally far from being upset by the adverse conclusions obtained from experiments on living human beings. Fick[6] found no change elicited in the excitability of nerves by the constant current. Eulenburg[7] confirmed Pflüger's laws. Erb[8] obtained at first quite opposite results, but having had his attention directed by Helmholtz to the likelihood of this having been caused by a peculiarity in distribution of the current in the uninjured human body, he repeated his experiments[9], and now attained results completely agreeing with those of Pflüger and Eulenburg. Runge[10] on the other hand arrived at quite opposite conclusions. It would seem pretty clear, however, that the complicated, not to say undeterminable, conduction-relations which exist in the living human body must cause a considerable difference between these results and those which rest on experiments made with isolated preparations of nerves, and that results of this kind cannot be adduced against Pflüger as proofs—so long at least as no question is taken into consideration excepting that of the way in which the normal excitability of a nerve is changed by a constant current of electricity.

[1] Budge, Archiv für patholog. Anatomie, xxviii, 1863, pp. 282–301.

[2] Valentin, Die Zuckungsgesetze des lebenden Nerven und Muskels, Leipzig, 1863, pp. 14, 65–86; Physiologische Pathologie der Nerven, i, Leipzig, 1864, pp. 134, 135; Zeitschrift für Biologie, viii, 1872, pp. 210–238; Moleschott's Untersuchungen, xi, 1873, pp. 169–181; Zeitschrift für Biologie, x, 1874, pp. 153–176.

[3] Schiff und Herzen, Moleschott's Untersuchungen, x, 1867, pp. 430–446.

[4] Lautenbach (under Schiff's direction), Archives des sciences physiques et naturelles, nouvelles période, lvii, 1877, pp. 88–99.

[5] Schiff, Moleschott's Untersuchungen, x, p. 436.

[6] Fick, Medicinische Physik, Zweite Auflage, 1866, p. 377.

[7] Eulenburg, Deutsches Archiv für Klinische Medicin, iii, 1877, pp. 117–142.

[8] Erb, ib. iii, 1867, pp. 271–273, and 513–524.

[9] Erb, ib. iii, pp. 525–528.

[10] Runge, ib. vii, 1870, pp. 356–384.

Of more weight than these investigations are those of Bilharz and O. Nasse, of Munk, of Grünhagen, of Wundt, and of Hermann and Bernstein, which have been conducted with all the care that researches of this nature demand. They also confirm in all essentials Pflüger's results, but serve at the same time partly to complete and partly to amend them, or to give a different theoretic significance to the facts discovered by him. A short glance at these will indicate their importance.

Under the direction of du Bois-Reymond, Bilharz and O. Nasse tested Pflüger's laws with mechanical stimuli[1]. For this purpose they availed themselves of Heidenhain's tetanomotor. The increase or diminution of the tetanus produced by it, when a constant current was passed in a given direction, served as a test of the change of excitability which then occurred.

Of course the test-stimulus injured the nerves to a very considerable extent. The nerve was hammered for six seconds continuously, and after each excitation got one to two minutes to recruit; yet in most cases it did not bear more than 6–8 successive stimulation experiments. So far as one can gather from the brief descriptions of the authors, they passed the polarising current in one direction only throughout each series of experiments.

With fresh nerves they established by this procedure the complete correctness of Pflüger's laws. As soon as the polarising current was closed a diminution took place at the positive pole in the tetanus elicited by the tetanomotor, at the negative pole an increase. When the experiment was continued the reverse relation set in; first there was no change when the current was closed, and after further application of the mechanical stimulus closing the current yielded precisely the opposite result, namely at the positive pole a strengthening, at the negative a weakening of the tetanus. The authors obtained just the same result when they produced local injury of the nerves with chemical substances. Afterwards Bilharz found[2] that other modes of injuring a nerve, for example the transmission of a very strong constant current through it, or the bringing of a red hot wire near it, &c. gave occasion to the same deviation from Pflüger's results.

From the brief account which the authors have published of individual experiments it is impossible to gather on what these

[1] Bilharz und O. Nasse, Archiv für Anatomie und Physiologie, 1862, pp. 66–83.
[2] Bilharz, Archiv für Anatomie und Physiologie, 1862, pp. 84–89.

deviations depend. Any how they cannot tell against Pflüger's laws, inasmuch as experiments on fresh nerves exhibited a complete accordance with them, as the authors expressly state ; and assuredly no significance can be attached to the adverse results given by nerves damaged in every imaginable way.

Moreover, a nerve is so delicate an organ that it is only with the greatest caution that we can draw conclusions from the phenomena which it presents after serious injury ; to which may be added that in investigations on the changes produced in nerves by a constant current a multitude of sources of error may easily disturb even the best arranged and most thoroughly thought out experiments.

Some years after, H. Munk came forward with considerations adverse to Pflüger's results, and on this ground, that the latter had in his investigations not taken into consideration the internal secondary resistance in nerves. Of the great work in which Munk was to have presented his experiments and his new doctrine [1] there has appeared only the first part, which deals with investigations on the secondary resistance in nerves. The question of changes of excitability evoked by the constant current Munk accordingly treats of only in a provisional communication [2].

Introducing as he did in the path of the current so great a resistance that the changes in resistance occurring in the course of experiment became relatively insignificant, he came to quite different conclusions from Pflüger. These and the theoretical view at which he has arrived he formulates in these words. 'The excitation of the nerve in consequence of the electrical current is due, firstly, to the direct displacement of the nerve-fluid in the direction of the current, and, secondly, to the return of the fluid, on interruption of the current, to those parts of the nerve from which it has been displaced.' . . . . 'The muscular contraction due to a given displacement of nerve-fluid is increased by a previously existing displacement of the same, when both displacements are in the same direction, but diminished when they are in opposite directions.'

Thus, according to Munk, the extrapolar excitability during closure of a descending current, is increased at the negative pole when the test-current is descending, diminished when it is ascending ; and so on.

[1] H. Munk, Untersuchungen über das Wesen der Nervenerregung, i, Leipzig, 1868.
[2] H. Munk, Archiv für Anatomie und Physiologie, 1866, pp. 369–390.

To estimate the value of these conclusions is clearly impossible as Munk has adduced no proofs to substantiate them. In his criticism of Pflüger he has moreover entirely overlooked the fact that the latter had also obtained by means of chemical stimuli the same results as he had got by testing with an electrical stimulus; and just as little does he take into account that Bilharz and O. Nasse had also found these confirmed by mechanical stimulation applied to fresh nerves. Under these circumstances we cannot regard his results as conclusive.

With all possible care and observance of minutiae Hermann[1] examined the changes of excitability, chiefly in the intrapolar region, with the object of substantiating the doctrine based on his investigation of the action-current in polarised nerves. 'Nerve excitability,' he says, 'increases in amount as we proceed to spots stronger in positive, or weaker in negative polarisation; in the reverse case it diminishes.'

In the introduction to his paper he directs attention to a circumstance, in itself clear enough, but which has been strangely overlooked by enquirers in this subject, namely, that, as the strength of the test-stimulus is increased, a point is reached where the influence of the constant current on the excitability of the nerve suddenly vanishes; and this point corresponds to such a strength of stimulus as evokes a maximal muscular contraction. With such a strength the muscular contraction can no longer be increased by katelectrotonus, for the very reason that it is at a maximum; its diminution through anelectrotonus also is trifling, and vanishes with such a strength of the stimulus as exceeds by only an insignificant amount that at which the maximal contraction occurs.

Further on in his paper Hermann gives an account of the investigations by which he supports his own doctrine and opposes Pflüger,—that is, not Pflüger's experiments, but his theoretical explanation of them. I pass over here one of Hermann's experiments, as to which he afterwards himself discovered that the result might be referred to a defect of arrangement[2], and shall only mention the others. These aim at proving:

1. That if the polarising current along with the seats of stimulation is brought nearer the muscle, while nothing else is altered, a diminution ensues in the influence of the polarising current for every stimulus applied on the near side of the indifference-point,

[1] Hermann, Archiv für die ges. Physiologie, vii, 1873, pp. 323–364.
[2] Hermann, ib. vii, 1873, pp. 497–498.

while its influence increases for every stimulus applied on the far side.

2. That at seats of stimulation lying far up, an approximation of the polarising current to the muscle is accompanied, first by a diminution, then by an increase of influence on the excitability.

3. That with strong polarising currents inhibition takes place at the negative pole; and if the excitatory effect has to pass this pole in the course of its propagation, muscular contraction must fail, and this as well with an ascending current and extrapolar stimulation as with a descending current and intrapolar stimulation. The last case should furnish a real experimentum crucis against Pflüger's view. With the first two it is not so, as other circumstances might influence the result, although such phenomena cannot be foreseen on Pflüger's theory.

The experiments instituted in proof of (1) were completely successful. When the fixed system of electrodes was brought nearer to the muscle, it appeared that with an ascending current the katelectrotonic increase of contraction became greater and its anelectrotonic diminution less, as also that with a descending current the relation was reversed.

With intrapolar stimulation Hermann found occasionally at the upper seat of stimulation a diminution, and at the lower an increase of muscular contraction. This, which would certainly form a decisive proof against Pflüger's theory, may however be explained on the ground that we have to deal with the same sources of error as in the experiments previously referred to, namely with the presence of nerve branches to the thigh, whereby, in the more distant position of the system of electrodes, the real indifference-point came closer to the proximal electrode than it did when the system of electrodes was brought nearer to the muscle.

In proof of (2) Hermann did not arrive at definite results. On the other hand, in the experiments which he instituted to obtain proofs of (3) he found, quite correctly, that with strong currents the muscular contractions fell off, and were entirely annulled when the excitation had to pass the negative pole. With an ascending current this could be explained on Pflüger's theory by inhibition at the positive pole, but this theory could not possibly explain why the influence of a stimulus applied in the neighbourhood of the negative pole should be diminished or annulled by a descending current.

Besides this it was only with currents of moderate strength that

Hermann found a diminution in the influence of an intrapolar stimulus at the positive pole of an ascending current; with weak currents, on the contrary, he obtained a reinforcement.

Particulars as to the strength of the polarising current, as well as with regard to the distance between its electrodes and those of the test-current, are, it is true, wanting in Hermann's paper; but the facts disclosed by him do nevertheless tell against Pflüger's theory, and cannot be explained in accordance with it, unless one assumes that the intrapolar test-electrodes were not near enough to the respective poles to lie in the anelectrotonic tract when the currents were weak; and, similarly, that with strong currents the anelectrotonus had extended to their position, although they lay tolerably near the negative pole. Obviously this cannot be decided without new experiments, at least so long as we have no detailed particulars on which to found conclusions.

Shortly after Hermann, Bernstein[1] took up this question. He employed maximal induction-shocks, and by their means investigated the change of excitability in the tract lying between the polarising current and the muscle. He moved the test-electrodes as close as possible to the nearest electrode of the polarising current; the distance between the electrodes of the latter being, on the other hand, considerable, namely 25 mm. The strength of the current was great, ranging from 4 Daniells with a derivation circuit of 10,000 rheochord units, up to 6 Groves without derivation. He sums up the result of his experiments thus—'When a constant current is passing along a nerve, the liberation of excitation is impeded at the positive pole, so that weak stimuli exercise less influence than under normal circumstances; but the maximum of the excitation elicited by powerful stimuli is greater. At the negative pole, on the other hand, the liberation of excitation is facilitated, so that weak stimuli have greater effect; but the maximum of excitation which can be liberated by strong stimuli is less.'

By a closer sifting of his results Bernstein endeavoured to show their accordance with Pflüger's theory, and expressly declared that they were no way in antagonism with its chief points, but rather served to confirm it.

Hermann[2] soon came forward in opposition to Bernstein. He had repeated Bernstein's experiments without succeeding in con-

[1] Bernstein, Archiv für die gesammte Physiologie, viii, 1874, pp. 40–60.
[2] Hermann, Archiv für die ges. Physiologie, viii, 1874, pp. 258–275.

firming his results, and he conjectured therefore that they were due to defective insulation, inasmuch as strong currents might easily enough have in part found their way to the nearest electrode of the test-current by conduction in the moist chamber, in which case its direction would of necessity be reversed. For further information as to the controversy the reader is referred to the originals[1].

All the investigations which I have so far referred to were in the main conducted by the same experimental methods. About the same time Wundt and Grünhagen sought to throw light on the question from a new point of view.

These enquirers had independently proposed to themselves to test the excitability of the nerve during the first moments after opening and closing the polarising current. With this object Wundt[2] availed himself of the pendulum myograph, and applied the test-stimulus at a short and accurately measured time after opening or closing of the polarising current. The essential part of his results is as follows—'Directly after the closing of the polarising current the excitability begins to rise through the whole length of the nerve. This increase of excitability continues, in the neighbourhood of the kathode, into the persistent katelectrotonic increase. In the neighbourhood of the anode the excitability mounts to a maximum and then again sinks gradually to make way for the anelectrotonic diminution. During a certain period, therefore, after closure of the constant current excitability is increased along the whole course of the nerve. This stage of increased excitability in both phases of electrotonus exceeds notably in duration the course of a muscular contraction with its associated stage of latent stimulation. At the moment the circuit is broken, with strengths of current which are not such as to introduce differences of conduction due to inhibitory processes, there occurs an excitation of which the intensity is the same whether on the kathodic or anodic side, and whether inside or outside of the poles. Along with this excitation, however, an inhibition sets in, which in part is occasioned by the remanent inhibition at the anode at closure of the current, and in part comes into existence at opening, in consequence of the occurrence of changes at the kathode which are

[1] Bernstein, Archiv für die ges. Physiologie, viii, pp. 498–505. Hermann, ib. ix, 1874, pp. 28–34.

[2] Wundt, Archiv für die ges. Physiologie, iii, 1870, pp. 437–440;—Untersuchungen zur Mechanik der Nerven und Nervencentren, i. Erlangen, 1871.

of the same nature as those which occurred at the anode at closure.'

In a provisional communication on his investigation, which, so far as I know, was not published, Grünhagen[1] very briefly made known the results he had obtained relative to the duration of the changes in excitability produced by a constant current. In this research he employed tetanus and its changes on closing and opening the current. He applied the test-stimulus between the polarising current and the muscle, and found that the tetanus in anelectrotonus fell off and in katelectrotonus increased, in such a way that in the first case the changes of excitability were longer in fully pronouncing themselves than in the latter. On the other hand, he could make out no change of excitability at the negative pole consequent on opening. An increase of excitability at the anode during the first moments after opening of the current, such as Wundt had observed, Grünhagen could not establish. Finally, he found an immeasurably short duration of increase in excitability at the kathode after interruption of the current. On these disagreements with Wundt's result we can lay no stress to the disadvantage of the latter, since the author has neither here nor since given a full statement of his experiments. The chief fact is that Grünhagen has confirmed Pflüger's laws in the most essential points.

The researches then which have been instituted since the appearance of Pflüger's work, to determine the changes of excitability in a fresh nerve elicited by a constant current, have, in essentials, confirmed Pflüger's results, and have, further, supplemented them with new investigations on the changes of excitability occurring directly after closure and opening of the current (Wundt, Grünhagen). The theoretical difference between Pflüger and Hermann is however still undecided; and the experiments instituted by the latter on the inhibitory influence of the negative pole with powerful currents constitute for the present very weighty objections to Pflüger's theoretical view.

Under such circumstances, and as hitherto no investigation of the changes of excitability has been instituted with purely mechanical stimuli, I considered that there were sufficient reasons for taking up the enquiry once more from this point of departure, the more so that the mechanical method of stimulation, with

[1] Grünhagen, Archiv für die gesammte Physiologie, iv, 1871, pp. 547–550.

the perfection to which it has recently attained, seemed to offer many and weighty advantages for experiments of this kind. In conducting these one has not, as with electrical stimuli, to fear an escape of electricity from the polarising to the test-current, or in the opposite direction. One can repeat the experiments in close succession without the nerve being thereby rendered useless, at the same time taking as measure of change of excitability individual muscular contractions, and not, as with chemical stimuli, exclusively tetanus; and, what is perhaps most important, one can get as near as one likes to the poles of the polarising current with mechanical stimuli and thus investigate it more satisfactorily than was ever possible with electrical or chemical stimuli. To this may be added that the mechanical stimulus is so completely different in its nature from the stimulus—the constant current—whose operation on the nerves it is the purpose of these investigations to determine.

Inasmuch as the changes of excitability outside the poles of the polarising current had been already so many times investigated by different enquirers, and as the results obtained—in so far as the methods used were free from error—had invariably confirmed those of Pflüger, I determined to apply myself specially to the changes in excitability of the intrapolar tract, and there again particularly to direct my attention to the pole nearest the muscle, that is, with an ascending current to the positive, and with a descending current to the negative pole, because in this way results could be attained in the simplest form and with least disturbance from other circumstances. At the same time I did not neglect to examine also the changes of excitability at other parts of the nerve, that there too I might test the correctness of Pflüger's laws by this method. My investigation separates itself accordingly into the following ten divisions.

1. *The changes of excitability at the negative pole of an ascending current—extrapolar.*

2. *The changes of excitability at the positive pole of an ascending current—extrapolar.*

3. *The changes of excitability at the negative pole of an ascending current—intrapolar.*

4. *The changes of excitability at the positive pole of an ascending current—intrapolar.*

5. *The change in site of the indifference-point with increasing strength of an ascending current.*

6. *The changes of excitability at the negative pole of a descending current—extrapolar.*

7. *The changes of excitability at the positive pole of a descending current—extrapolar.*

8. *The changes of excitability at the negative pole of a descending current—intrapolar.*

9. *The changes of excitability at the positive pole of a descending current—intrapolar.*

10. *The change in site of the indifference-point with increasing strength of a descending current.*

The experimental arrangements were as follows (see Fig. 1).

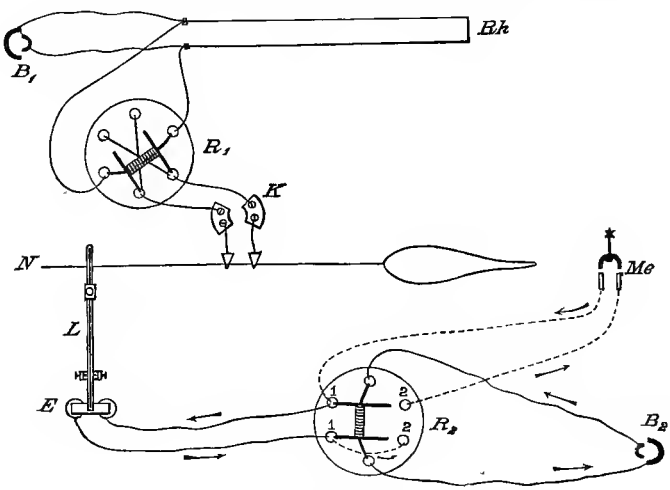

Fig. 1.

From the battery (B_2) the current passes to the electro-magnet (E), which elevates the lever of my new mechanical stimulation-apparatus, which I employed in these experiments[1] (see Fig. 2). This current then passes to a Pohl's reverser without the cross wires. If the arms of the reverser dip into the mercury cups 1, the current passes directly to the electro-magnet, and the lever is held sus-

[1] Cf. Tigerstedt, 'En ny metod för mekanisk retning af nerver' Nordiskt, Medicinskt Arkiv, xiii, 1881, Nr. 12. A description of this method will shortly appear in the Zeitschrift für Instrumentenkunde.

pended so that it does not rest on the nerve. If, however, the arms of the reverser are placed in the cups of mercury 2, the current is compelled, before reaching the electro-magnet, to pass through the metronome (M), which by its oscillations opens and closes the circuit to the electro-magnet. Each time the circuit is broken the lever falls on the nerve and stimulates it. When the circuit is closed by the swing of the metronome in the opposite direction, the lever rises again from the nerve. The direction of the current is indicated in the figure by the arrows.

The polarising current I obtained from a battery of Meidinger's Elements (B_1). First it was carried to a du Bois-Reymond's rheochord (Rh), where it divided, then to a Pohl's reverser, from there to a du Bois-Reymond's key (K), and then to the nerve. The current was closed and broken by means of the key, its strength being graduated in the usual way by means of the rheochord.

The current was, of course, led through the nerve in the ordinary way by unpolarisable electrodes. To make them properly suit my apparatus, I gave them a different form from what they usually have; and I take occasion here to describe them, as they seem to me more practical and handier for stimulation experiments than most of the others in use.

Each consists simply of a box of ebonite $2\frac{1}{2}$ centims high, the base of which is 1 centim square. Underneath it is provided with two steel prongs screwed in, by means of which it can be fixed on the cork plate of my lever-apparatus, outside the bed for the nerve. The inside of the trough is filled with paraffin to prevent any contact between the clay and the steel prongs. The clay, having been previously soaked with a 0·6 % solution of common salt, is shaped with the hands into long rolls, which are then placed in the trough, with their ends bent forwards. These ends can afterwards have such a form given them as may best suit each particular experiment. In the clay is stuck a glass tube, which is filled with a concentrated solution of sulphate of zinc; and into this is introduced a well-amalgamated slip of zinc, which is connected by means of a conducting wire with the wires of the battery (Fig. 1 B_1).

In certain experiments, where it was of primary consequence to bring the mechanical exciter quite close to the electrodes, I carried the current to the nerve through a strip of filter-paper soaked in a 0·6 % solution of common salt, which was attached to the unpolarisable electrodes just described.

To keep it moist, the nerve was placed with the tract to be subjected to the mechanical excitation lying on a strip of filter-paper soaked in a 0·6 % solution of common salt. When the intrapolar tract was being excited this strip included nearly the whole distance between the electrodes. By this arrangement, it is true, the branch of the current which passed through the nerve was somewhat weakened, but this could be made up for by means of a stronger current. Besides, in this way not only did

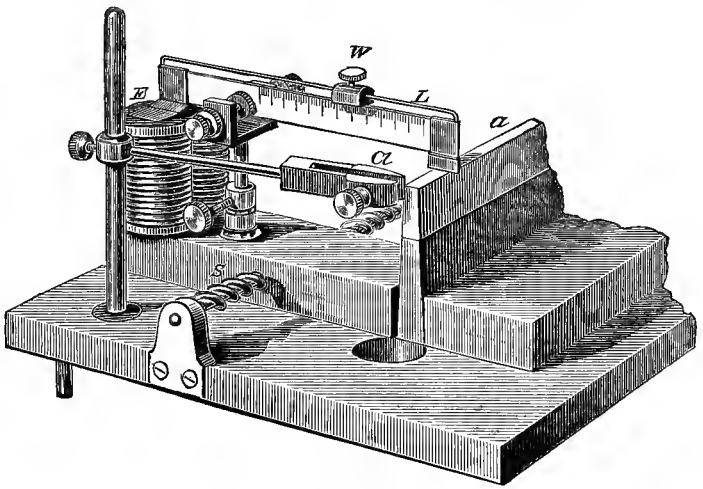

Fig. 2.

TIGERSTEDT'S INSTRUMENT FOR MECHANICAL EXCITATION OF NERVES.

[The femur of the 'nerve muscle preparation' is held by the clamp *Cl*. The nerve lies on the anvil *a*. Whenever the current through the electro-magnet *E* is broken, the edge of the hammer *L* falls on the nerve. The degree of excitation thus produced is regulated by the position given to the sliding weight *W*. The distance of the seat of excitation from the muscle can be varied by means of the spiral screw *S*. The whole instrument is enclosed in a glass case so that the preparation is in moist air.]

I succeed in keeping the nerve moist, but I obtained also a certain measure of security against the sources of error which, in consequence of the varying thickness of the nerve, attended Hermann's experiments on the changes of excitability produced by a constant current[1]. In some experiments specially indicated, where it was important to have the polarising current as strong as possible, I put no paper under the nerves.

In those experiments in which paper was used the nerve was never stimulated outside the sheet on which it lay. False results, produced by the different strengths of the current in the rest of

[1] Hermann, Archiv für die ges. Physiologie, vii, 1873, pp. 497–498.

the nerve, and also in the extremely short piece of nerve lying between the paper and the electrodes, are therefore precluded.

The stimulation experiments were arranged in the following order. It was ascertained what strength of mechanical stimulus would produce a contraction of a suitable magnitude, that is, a moderately strong contraction with stimulation in the neighbourhood of the positive pole, a moderate or weaker one with stimulation near the negative pole. This having been found, the metronome was set in motion, and the muscle had now to trace out about half a dozen contractions on the cylinder of the myograph. Thereupon, the metronome continuing to open and close the current to the electromagnet, the polarising current was at once closed, and the muscle had again to trace out five or six contractions. After this the polarising current was opened, and half a dozen muscular contractions recorded uninfluenced by the polarising current. Following the same order, I continued the experiment for some time, the number of repetitions depending, partly on the endurance of the nerve, partly on the purpose for which the experiment was undertaken. At the same time the strength of the polarising current was sometimes varied. Every experiment relating to change of excitability under the influence of the current, was preceded and followed by an experiment in which the mechanical excitation acted alone.

Throughout each experiment the mechanical excitation continued to act in the order given to it. By this arrangement I could study the course of the changes of excitability more closely than in any other way at my disposal, as well while the current was closed as when it was open. The metronome interrupted the current to the electromagnet three times in two seconds on the average. I was unable to determine more minutely the relations of excitability during the first moments after the opening and closing of the current. This, however, lay outside my purpose, which was to investigate the persistent changes of excitability during closure of the current and after its discontinuance.

To show that the nerve completely tolerates mechanical excitation when thus conducted, I made a number of experiments with mechanical stimulation alone. These proved that the nerve possesses a much greater toleration of mechanical stimulation than has hitherto been supposed, and greater than my own earlier experiments had shown[1]. Besides, they showed that the contractions

[1] Tigerstedt, Studien über mechanische Nervenreizung, i, Helsingfors, 1880, p. 34.

decline regularly and slowly when mechanical excitation is continued. This proves that mechanical stimulation is in reality quite specially adapted for the study of changes of excitability in nerves. In consideration of the importance of this matter, I shall here cite one or two of these experiments.

Experiment A. Distance from the muscle of the point of stimulation (plexus) 39 mm.; position of the sliding weight on the arm of the lever 22; 3 stimulations in 2 seconds; number of stimulations 420.

Experiment B. 1. Distance from the muscle of the spot stimulated (plexus) 42 mm.; position of the sliding weight on the lever arm 25; 110 stimulations in one minute; number of stimulations 330.

2. The same nerve. Distance of the spot stimulated from the muscle 26 mm.; rhythm and strength of the stimuli as before; number of stimulations 139.

The muscular contractions were in some experiments recorded on a registering apparatus of Marey's, provided with Foucault's regulator; in others on a recording cylinder constructed by Lovén, which last was worked by a water-motor with the greatest regularity.

I used an elastic recording lever constructed by Lovén, which magnified the muscular contractions 3·5 times.

The experiments were continued from October 1881 up to January of this year, and were made on specimens of Rana esculenta which had been sent in autumn from Berlin. Throughout each experiment the polarising current was constantly in one direction. In these investigations it was important to enquire into the changes of excitability of the nerve evoked by a current with a certain fixed direction. In order that the result should come out as clearly as possible, it was imperative that the direction of the current should remain unaltered for each experiment. Considering how delicate and easily destroyed the nerve substance is, one must use the greatest circumspection to avoid having it more destroyed or injured than is indispensably necessary for the purposes of the experiment. If, however, the direction of a constant current is frequently changed, it may easily happen that the results are disturbed. I am convinced for my part that the numerous irregularities which many enquirers have found, depend to a considerable extent on their having too frequently changed the direction of the current. In every experiment the conditions must be made as simple as possible, and it is better to use several nerves than seek to get everything from one nerve. Such experiments may often give no results.

In the description of the experiments these abbreviations are used.

$+P$ = the distance of the positive pole from the muscle.
$-P$ = the distance of the negative pole from the muscle.
E = the distance of the spot stimulated from the muscle.
Rh = the number of rheochord units in the derivation circuit[1].
γ = the position of the sliding-weight on the lever.

Partly to represent the results more clearly, partly to give sufficient proof of the superiority of the mechanical method of stimulation for investigations relating to the general physiology of nerves, I have appended to the description of the experiments reproductions of my curves in fairly large number[2].

1. The extrapolar changes of excitability at the negative pole of an ascending current.

With weak and moderate currents the excitability is considerably increased. This increase attains its full strength directly after the current is closed. An intensity of the stimulus which shortly before called forth quite feeble muscular contractions or none at all, now evokes very strong ones. The increased excitability is observed during the whole time the current is closed. Nevertheless the contractions diminish in course of time, though to a very slight extent, sometimes indeed scarcely appreciably, and in many cases not at all. If the current is opened the contractions resume their previous magnitude. No inhibition showed itself with the conditions under which my experiments were conducted; on the contrary a slight augmentation of excitability set in after the current was opened. This increase, however, as already pointed out, is trifling and is not always distinctly apparent. It lasts a longer or shorter time and gradually disappears.

During the closure of the current the increase is greatest at the negative pole, and from thence stretches upwards. The greater the strength of the polarising current, the greater also is the change of excitability, and the more distinctly do its attendant phenomena appear. At the same time it extends over larger tracts of the nerve.

If the experiment is repeated in such a way that the polarising current is opened and closed in regular succession, while its

[1] Cf. Hermann, Archiv für die ges. Physiologie, vii, 1873, p. 333.

[2] These have been omitted, as it appeared that the experimental results could be understood without them.

strength with that of the stimulus remains all the time unaltered, the muscular contractions evoked under the influence of the polarising current remain of uniform amount through the whole of the long series. The effect due to exhaustion of the nerve in consequence of stimuli following each other in close succession is by no means so pronounced when the current remains closed as when the nerve is exposed to mechanical stimulation only.

The increase of excitability occurs also with perfect distinctness even when the current produces make- and break-contractions. I have not made experiments with stronger currents, as no observer has questioned that with stimulation in the presence of a powerful ascending current the muscular contractions fall off and disappear. It is only the theoretical explanation of the phenomenon about which there is disagreement.

Examples.

Experiment 1.

$+P = 24$; $-P = 40$; $E = 44$; 3 Meidinger, $Rh. = 45$.

The mechanical stimulus by itself generated no contractions. The constant current produced a strong make- but no break-contraction. Under its influence the mechanical stimulus called forth strong contractions of uniform height, which disappeared after the current was opened, but returned in even greater strength when it was again closed.

Experiment 2.

$+P = 14$; $-P = 30$; $E = 35$; 1 Meidinger, $Rh. = 160$; $\gamma = 30$.

a. The mechanical stimulus evoked only small contractions. The constant current produced a make- but no break-contraction. Under its influence the muscular contractions elicited by the mechanical stimulus at once gained double strength, and during the whole time the current was passing kept at nearly the same height. When the current was opened, the contractions were very slightly stronger at first, but soon declined to their former strength.

b. If the nerve was now stimulated somewhat nearer to the pole ($E=34$), other conditions being the same, the mechanical stimulus evoked no muscular contractions, but, under the influence of the current, these showed themselves much stronger than in *a*, though not of the same height all the time. When the current was interrupted they at once disappeared.

Experiment 3.

$+P = 10$; $-P = 19$; $E = .25$; 2 Meidinger, $Rh. = 450$; $\gamma = 20$.

a. The mechanical stimulus produced no muscular contractions; the constant current produced a make- but no break-contraction. Under the influence of the current there occurred remarkably large contractions of uniform strength, which instantaneously disappeared when the current was opened, to return when it was again closed.

b. When the nerve was subjected to the same intensity of mechanical stimulation somewhat higher up ($E = 26$), the contractions that took place during the passage of the current were not nearly so strong as in *a*; and on the other hand they underwent a slow decrease during each period that the current was closed.

c. When the polarising current was strengthened (2 Meidinger, $Rh. = 1{,}450$), so that contraction took place when it was opened the contractions were notably stronger on stimulation of the spots above mentioned than they previously were, or even than in *a*. The slow decline of the contractions with continuance of the current can here be clearly recognised. In each experiment of these series, (*a*, *b*, *c*,) however, the contractions elicited during the action of the constant current are always of nearly the same height. Thus in *c* one can make out no diminution of the contractions at the end as compared with those at the beginning, but on the contrary the latter are a little less than the former; and yet the nerve had been subjected during nearly 160 seconds to at least 240 stimulations.

2. The extrapolar changes of irritability at the positive pole of an ascending current.

The excitability of the nerve is considerably diminished. An intensity of the stimulus, which a short time previously elicited very large contractions, now causes quite small ones or none. This diminished excitability lasts all the time the current is closed. In the circumstances under which my experiments were conducted the diminution set in directly the current was closed. At the same time the first contraction was sometimes greater than those following it. Occasionally, on the other hand, while the current continued to flow through the nerve, the muscular contractions increased from their first minimum, only however to a trifling extent and often scarcely perceptibly, in some cases not at all. When the current is opened the muscular contractions return to their original strength, without at the same time any recognisable inhibition exhibiting itself in the first moments. On the contrary, there appears in the nerve a

slight increase of excitability, which, however, is not very great and in many cases is quite absent. It persists for a longer or shorter time and then gradually disappears.

During the passage of the current the diminution of excitability is greatest at the positive pole, and falls off as we move from this point lower down. The stronger the polarising current, the greater also is the diminution of excitability, and the greater the nerve-tract over which it extends.

If the experiment is repeated in such a manner that the polarising current is closed and opened in regular succession, while the strength of the current and that of the stimulus remain all the time constant, the contractions evoked under the influence of the polarising current in most cases get weaker and weaker, while those produced by the mechanical stimulus alone keep throughout at their original height, and do not decline in consequence of exhaustion of the nerve or muscle nearly so quickly as under ordinary circumstances.

Examples.

Experiment 4.

$+P = 26$; $-P = 37$; $E = 9$; 3 Meidinger, $Rh. = 4500$; $\gamma = 30$.

a. The mechanical stimulus produces very strong muscular contractions: the polarising current both make- and break-contractions. Directly after the current is closed the contractions fall to less than half their previous magnitude, and rise somewhat with the continuance of the current, but to a very trifling extent and quite slowly. When the current is opened they return to their former strength, which they retain until it is again closed, when once more a diminution occurs. In the course of the experiment the contractions produced under the influence of the polarising current become feebler and feebler gradually, though not quite regularly, while those evoked by the mechanical stimulus alone retain their original magnitude, and this although the number of stimulations in this experiment amounts to 120.

b. Under conditions otherwise quite similar, but with a weaker strength of the polarising current (3 Meidinger, $Rh. = 1500$), which however still elicits make- and break-contractions, the nerve is stimulated nearer to the positive pole ($E = 15$). The contractions produced by the mechanical stimulus, which are of the same strength as in *a*, disappear completely under the influence of the current, and again reach their original height as soon as the current is opened.

Experiment 5.

$+P = 22{\cdot}5$; $-P = 36$; $E = 19$; 3 Meidinger, $Rh. = 500$; $\gamma = 20$.

a. The mechanical stimulus generates moderately strong contractions; the polarising current both make- and break-contractions. Under its influence the muscular contractions of the first two series vanish instantaneously. Later on they no longer vanish when the current is closed, but they become at once quite small and remain so during the whole time the current is passing; when the current is opened they again reach their former height, but there is no further rise. Even in the last series of all the contractions retain close upon their original magnitude, although the number of stimulations amounts to about 140.

b. The strength of the polarising current is considerably increased (3 Meidinger, $Rh. = 10{,}000$), and the nerve is stimulated somewhat nearer to the muscle ($E = 16$). Under the influence of the current the contractions completely vanish.

c. The stimulus is brought still nearer to the muscle ($E = 14$), and the strength of the polarising current modified till it coincides with that in experiment *a* (3 Meidinger, $Rh. = 500$). No change occurs in the strength of the contractions either when the current is closed or when it is opened.

3. The intrapolar changes of excitability at the negative pole of an ascending current.

With weak and moderate currents the excitability of the nerve is considerably heightened. This increase appears in its full strength directly after the current is closed. An intensity of stimulation, which shortly before called forth only slight contractions or none, now produces strong ones. This increased excitability exhibits itself the whole time the current is passing; it is however noticeable, especially in the case of nerves which have undergone repeated experiments according to this arrangement, that with the current closed the contractions very slowly fall off; the decrease is, however, unimportant, and does not always occur. As soon as the current is opened the contractions return to their original height. In the circumstances under which I have conducted my experiments, I have not been able to make out any inhibition in the period immediately following. On the contrary, there is often exhibited a heightening of the excitability, which, however, is never particularly great; this too can often not be clearly proved.

During closure it is at the negative pole that the increase of

excitability is greatest. It increases with the strength of the current till the latter has reached a certain grade.

If the experiment is pretty frequently repeated the enhancement of excitability remains much the same during each closure of the current, even when the contractions elicited by the mechanical stimulus alone fall off.

EXAMPLES.

Experiment 6.

$+P = 20$; $-P = 40$; $E = 37{\cdot}5$; 3 Meidinger, $Rh. = 92$; $\gamma = 17$.

a. The mechanical stimulus produces weak muscular contractions; the polarising current only a make-contraction. Under its influence the contractions grow to more than double their size, and during the passage of the current show an exceedingly slight falling off. As soon as the current is opened the contractions fall off, but are still somewhat greater than they originally were. The same phenomenon is repeated if the experiment is gone through several times in succession.

b. The nerve is stimulated somewhat farther up with the same strength of mechanical stimulus ($E = 38$). The polarising current is now stronger (3 Meidinger, $Rh. = 150$). With this arrangement the contractions rise from a very low point to an equal height with those in *a*. On opening the current they disappear completely, to reach the same strength as before when the current is closed. In other respects the phenomena of *a* are here repeated.

Experiment 7.

$+P = 10$; $-P = 30$; $E = 29$; 1 Meidinger, $Rh. = 1950$; $\gamma = 5$.

The mechanical stimulus produces exceedingly slight contractions; the polarising current only make-contractions. Under its influence there occur strong, almost maximal, contractions, which keep throughout at the same height, and instantaneously cease when the current is opened. When the current is closed the strong contractions set in afresh. After the nerve has rested for a minute the experiment is repeated from the beginning in the same way. There now appear, after the current has been twice closed and opened, small muscular contractions, showing that the excitability of the nerve has increased.

Under the influence of the polarising current the same strong contractions as before take place; they are now however not of so uniform a height as at the beginning of the experiment, but display slight irregularities.

4. The intrapolar changes of excitability at the positive pole of an ascending current.

The excitability of the nerve is considerably diminished with all strengths of the current, even with the weakest. Frequently this diminution does not show itself on the instant, but the muscular contractions gradually fall off under the influence of the current, so that the first are somewhat greater than those which follow. This diminished excitability is exhibited all the time the current is closed. It pretty often happens that meanwhile the muscular contractions begin gradually to rise, but this rise is always inconsiderable, and in certain cases is imperceptible. With the current open the contractions instantaneously increase. At the same time no inhibition can be demonstrated. On the contrary there occurs a trifling increase of excitability, which is however sometimes quite unnoticeable. It lasts a longer or shorter time, and then gradually disappears.

The diminution of excitability when the current is closed is greatest at the pole itself. It increases with the strength of the polarising current.

If, under the same external circumstances, repeated experiments are made, the diminution of excitability generally increases, though very inconsiderably. Sometimes, too, it may be observed that the diminution falls off, but at the same time the contractions evoked by the mechanical stimulus alone have become stronger. In general these maintain their original height or undergo a very slight increase; now and then it may happen that they fall off, but this is very unusual.

EXAMPLES.

Experiment 8.

$+P = 8$; $-P = 34$; $E = 9$; 2 Meidinger, $Rh. = 50$; $\gamma = 20$.

a. The mechanical stimulus produces weak contractions. The polarising current evokes neither make- nor break-contractions. Under the influence of the current the contractions instantly vanish and reappear only when the current is opened. They are then a trifle weaker.

b. The same nerve is stimulated somewhat higher up, $E = 10$, with the same strength of mechanical stimulus, and the polarising current is made still weaker (2 Meidinger, $Rh. = 42$). Even then the contractions cease under its influence and resume their previous strength only when the current is again opened.

c. The current is still weaker (2 Meidinger, $Rh. = 30$). The same spots are stimulated as in *b*, and under the same circumstances. Now the contractions no longer cease, but they fall off perceptibly in strength. On opening the current they regain their former intensity. If it is still further weakened, the current produces no change in the contractions.

Experiment 9.

$+P = 15$; $-P = 34$; $E = 17$; 2 Meidinger, $Rh. = 44$; $\gamma = 30$.

a. The mechanical stimulus excites weak contractions. The polarising current produces neither make- nor break-contractions. Yet under its influence the muscular contractions instantaneously vanish, and reappear in their former magnitude directly after the next break of the current.

b. The nerve is excited with the same strength of mechanical stimulus, but somewhat further from the pole ($E = 19$). With the same intensity of the polarising current the muscular contractions now do not disappear, but they fall off considerably in height. When the current is broken they again reach their former magnitude.

Experiment 10.

$+P = 17$; $-P = 36$; $E = 20$; 3 Meidinger, $Rh. = 5000$; $\gamma = 30$.

The mechanical stimulus excites tolerably strong contractions; the polarising current produces both make- and break-contractions. Under its influence the contractions disappear. Slight traces of them may, however, be remarked during the first moments after interruption of the current. As soon as the current is opened the contractions reappear and they are then somewhat stronger than they were before closure, but sink by degrees to their original strength.

Experiment 11.

$+P = 15$; $-P = 34$; $E = 22{\cdot}5$; 3 Meidinger, $Rh. = 4530$; $\gamma = 30$.

a. The mechanical stimulus excites moderate contractions; the polarising current make- and break-contractions. Under its influence the contractions decline almost to complete evanescence. The decrease is not so great directly after the current is passed as it is later on. On opening the current the contractions reappear in their original intensity. The current is again closed, and now the muscular contractions completely disappear; but in the further course of the experiment, the current continuing to pass, minute contractions

again occur. When the current is opened, these for some time grow more minute. Finally, they again mount so that they overstep their original height not a little. When the polarising current is closed, they do not altogether disappear, but merely decline to a minimum.

b. The nerve is excited with the same strength of stimulus, but nearer to the positive pole ($E = 21$). The muscular contractions are now fairly strong. Under the influence of the polarising current they wholly disappear, but show themselves as large as before so soon as it is again opened. If the experiment is repeated in this way several successive times, the muscular contractions evoked by the mechanical stimulus alone become a little greater than they originally were.

5. The change of position of the indifference-point with increasing strength of an ascending current.

In order to investigate how the excitability at different points of the intrapolar tract alters with varying strengths of the polarising current, I proceeded in the following way. I first investigated how a very weak current (1) changed the excitability of the nerve at a spot (*A*) in the neighbourhood of the positive pole. If it appeared that at this spot the excitability was heightened, I raised the strength of the polarising current until the excitability was here visibly lowered by the current (2). Thereupon I examined how the excitability was changed by the current (2) at another spot (*B*) higher up. If the excitability there showed itself unchanged or heightened, the strength of the current was again raised till a diminution of the excitability set in. After that I ascertained what relation the excitability at a spot (*C*) lying still higher up bore to the strength of the current (3) last mentioned.

If Pflüger's view that with an increasing strength of current the indifference-point shifts from the positive towards the negative pole represented the real state of the case, the excitability at a point not far from the positive pole would be raised by very weak currents; while, if the strength of the current increased, a diminution of excitability would display itself at this spot, at the same time that another spot lying higher up would still be in the stage of increased excitability; and so on.

If therefore, as I gradually raised the strength of the current the seat of stimulation gradually shifted from the positive to the negative pole, I was necessarily in a position to prove that

the condition of diminished excitability extended more and more over the intrapolar tract of the nerve. Whether the decrease of the contractions which took place with a given strength of current on stimulation of a given spot (A) depended on a hindrance occurring at the positive pole to the conveyance of excitation to the muscle, or on an actual decrease of excitability at this spot, I thought might be decided by stimulating a spot (B) higher up, which, supposing the last hypothesis confirmed, would necessarily manifest a heightened or unaltered excitability. The justness of this assumption was established in the most convincing manner.

With regard then to the changes of excitability in the intrapolar tract, in so far as these depend on the strength of the polarising current, Pflüger's law holds absolutely. The more the strength of the polarising current is raised, the greater is the portion of the intrapolar tract over which the condition of diminished excitability extends, and the shorter is that portion of the tract which exhibits an increase of excitability; or, in other words, with increasing strength of the polarising current the indifference-point moves from the positive toward the negative pole. With quite weak currents the condition of diminished excitability shows itself only in the immediate neighbourhood of the positive pole, while far the larger portion of the intrapolar tract manifests an increased excitability. With stronger currents, on the other hand, the excitability is lowered over the greater part of the intrapolar tract, and only the smaller part exhibits enhanced excitability.

In consequence of the inhibition which sets in at the positive pole with strong polarising currents, the investigation into the increase of excitability at the negative pole can, of course, not be pursued beyond certain strengths of the polarising current.

Examples.

Experiment 12. $+P = 11$; $-P = 32$; 2 Meidinger; $\gamma = 10$.

a. $Rh. = 220$; $E = 13$. The mechanical stimulus produces weak currents. The constant current excites a make- but no break-contraction. Under its influence the magnitude of the contractions elicited by the mechanical stimulus is unaltered.

b. $Rh. = 220$; $E = 18$. Here the mechanical stimulus excites only small contractions, but these increased considerably under the influence of a current of equal strength with that in *a*.

c. $Rh. = 300$. With increased strength of the current, on the other hand, no change is produced in the magnitude of the contractions.

d. $Rh. = 400$. When the current is still further increased it quite annuls the muscular contractions. Here be it observed that in the experiments *b*, *c*, *d* the same part of the nerve was used ($E = 24$).

e. The nerve is now stimulated somewhat higher up ($E = 24$). Under the influence of the constant current, which is now of the same strength as in *d*, the muscular contractions are, it is true, diminished, but this diminution does not by a long way reach the same amount as in *d*.

f. Stimulation is now applied nearer to the negative pole ($E = 25$). The mechanical stimulus now produces only slight contractions, which under the influence of the same current as in *d* and *e* increase by a very little. Throughout the experiment the strength of the mechanical stimulus has been unaltered.

Experiment 13. $+P = 11$; $-P = 33$; 2 Meidinger.

a. $E = 15$; $Rh. = 90$. The mechanical stimulus causes only small contractions. The constant current produces a make- but no break-contraction. Under its influence the contractions elicited by the mechanical stimulus vanish forthwith.

b. $E = 18$; $Rh. = 90$. The mechanical stimulus causes only feeble contractions. These are not modified by a constant current of the same strength as in *a*.

c. $E = 18$; $Rh. = 200$. Stimulation is continued at the same spot, but the strength of the polarising current is increased. On closure, the muscular contractions at once vanish, to reappear when the current is opened.

d. $E = 29$; $Rh. = 200$. The mechanical stimulus here excites fairly powerful contractions, which are not in the least altered by the action of a current having the same strength as in *c*.

e. $E = 16$; $Rh. = 60$. Finally the nerve is stimulated close to the positive pole. The strength of the polarising current is quite inconsiderable. When this is closed no change occurs in the strength of the contractions. Throughout the experiment the mechanical stimulus remained of the same strength.

6. The extrapolar changes of excitability at the negative pole of a descending current.

The excitability of the nerve is considerably increased. This

tractions, as also does the constant current, but only when it is closed, and not when it is opened. Under the influence of the constant current the contractions produced by the mechanical stimulus assume their maximum directly, and keep at this strength as long as the current is closed. When it is opened they diminish till they have reached their former grade. Under the influence of the polarising current the contractions remain constantly alike on repetition of the experiment, although the mechanical stimulus by itself elicits even weaker contractions, which gradually fall off, quite according to the law established by experiments on nerve-exhaustion.

Experiment 16. $+P = 40$; $-P = 28$; 3 Meidinger; $\gamma = 22$.

a. $E = 25$; $Rh. = 25$. The mechanical stimulus occasions no contractions; the polarising current none either. Under its influence, however, weak contractions are caused by the mechanical stimulus, which throughout the closure of the current keep at the same height, and when the current is opened straightway vanish.

b. $E = 23$; $Rh. = 119$. The mechanical stimulus brings about no contractions; the constant current a make- but not a break-contraction. Under its influence the mechanical stimulus causes weak contractions, about the same as in *a*; these have a uniform height while the current is closed, and vanish instantaneously when it is opened.

c. $E = 21$. The mechanical stimulus by itself causes no contractions. Under the influence of a current of the same strength as in *b* contractions occur which are somewhat smaller than the former.

7. The extrapolar changes of excitability at the positive pole of a descending current.

The excitability of the nerve is considerably lowered. Such an intensity of stimulus as but a short time previous evoked quite strong muscular contractions, now produces only insignificant contractions or none at all. In the circumstances under which I undertook my experiments this diminution showed itself directly after closure of the current; at the same time the first contraction was sometimes a little greater than its successors. If the current is led through the nerve for some length of time the muscular contractions gradually increase, but this takes place very slowly and sometimes scarcely appreciably, in many cases not at all. When the current is opened the contractions sink to their previous height. At the same time no inhibition can be demonstrated. On the contrary a slight increase of excitability takes place, which is yet never of consequence and is often altogether absent.

increase is shown in its full amount directly after the current is closed. An intensity of stimulus which previously elicited very slight contractions or none, now causes very strong ones. This increased excitability lasts the whole time the current is passing. At the same time the muscular contractions get smaller, although only to a slight extent, and often there is no diminution. On the cessation of the current the contractions decline to their previous size.

In the circumstances under which my experiments were performed no diminution of excitability set in after the current was opened. A slight increase sometimes occurs, but in general the contractions return to their previous height after the current is opened. As long as the current is closed the rise in excitability is greatest at the negative pole, and from there it falls off towards the muscle.

The stronger the polarising current the greater also is the increase of excitability, and the greater the tract of nerve over which it extends.

If the experiment is repeated in such a way that closure and opening succeed one another regularly, while the strength of the stimulus and of the current remain constant throughout, the contractions exhibited under the influence of the polarising current remain steadily uniform through the whole series, even though the contractions evoked by the mechanical stimulus alone might gradually fall off through exhaustion of the nerve.

Examples.

Experiment 14.

$+P = 30$; $-P = 17$; $E = 16$; 3 Meidinger, $Rh. = 85$; $\gamma = 32$.

The mechanical stimulus occasions moderate contractions: the constant current make- but not break-contractions. Under its influence the contractions evoked by the mechanical stimulus rise to about the maximum. At the same time the first contraction produced after passage of the current is a little stronger than its successors, which undergo an exceedingly slow decline. After the current is opened the contractions return directly to about the same height as they previously had.

Experiment 15.

$+P = 36$; $-P = 24$; $E = 22$; 3 Meidinger, $Rh. = 100$; $\gamma = 15$.

The mechanical stimulus produces very strong muscular con-

While the current is closed, the change of excitability is greatest at the positive pole, and falls off in the direction of the spinal cord. The stronger the polarising current the greater is the diminution of excitability, and the greater also is the tract of nerve over which it extends. If the experiment is repeated in such a way that the polarising current is closed and opened in regular succession while the strengths of the stimulus and of the current remain the whole time unmodified, the muscular contractions in each group become smaller and smaller, while the contractions elicited by the mechanical stimulus alone retain all the time their original height, and do not decline nearly so quickly as they usually do in consequence of nerve exhaustion.

EXAMPLES.

Experiment 17.

$+P = 33$; $-P = 7$; $E = 41$; 3 Meidinger, $Rh. = 160$; $\gamma = 42$.

The mechanical stimulus occasions strong contractions; the constant current make- but no break-contractions. Under its influence the contractions drop to half their initial amount. The experiment is repeated time after time, and now the contractions produced under the influence of the constant current grow always slighter, while those occasioned by the mechanical stimulus alone retain the whole time near upon their original height. Finally, they cease completely when the current is passed. In several series it is observed that the first stimulation after closure of the current produces a greater effect than any of its successors, but that, on the other hand, later on, with the continued flow of the current along the nerve, the contractions increase quite slowly.

Experiment 18. $+P = 28$; $-P = 14$; 3 Meidinger; $\gamma = 20$.

a. $E = 35$; $Rh. = 40$. The mechanical stimulus produces tolerably strong contractions; the polarising current make- but no break-contractions. Under its influence the contractions elicited by the mechanical stimulus diminish to half their original strength. As the experiment proceeds the contractions elicited under the influence of the constant current fall off more and more, and at last disappear, while those occasioned by the mechanical stimulus alone retain all the time their initial magnitude.

b. $E = 38$; $Rh. = 100$. Under the influence of a stronger current than that in *a*, which yet produces only make-contractions, the contractions caused by the mechanical stimulus fall to half their

previous size. When the experiment is repeated they finally disappear. At the same time the contractions are not instantaneously annulled, but during the first moments after closure of the current small contractions still show themselves, disappearing with continuance of the current.

c. $E = 41$; $Rh. = 100$. With the same strength of polarising current as in *b* the diminution of the contractions is far less, the distance of the spot stimulated from the pole being greater.

d. $E = 40$; $Rh. = 270$. An increased strength of current, on the other hand, makes the contractions at once disappear at a spot lying only 1 mm. nearer the pole.

e. $E = 42$; $Rh. = 270$. This is also the case 2 mm. higher up. After a little small contractions show themselves for a time, the current remaining closed.

8. The intrapolar changes of excitability at the negative pole of a descending current.

The excitability was raised with every strength of current tried, i. e. up to 10 Meidinger's elements inclusive. This rise instantaneously assumes its full amount when the current is closed. An intensity of the test-stimulus, which shortly before evoked quite small contractions or none, now produces quite strong ones. This increased excitability continues the whole time the current is closed. Yet it is to be observed that the contractions gradually decline during closure of the current, especially with nerves on which repeated experiments have been performed with reference to this point. This decrease, however, is in most cases exceedingly slight, and often does not appear at all. When the current is opened the contractions fall to their original height; when weak currents were opened no diminution of excitability presented itself in the circumstances under which I carried on my experiments. On the other hand, in the first moments after a stronger current is opened, an evident diminution of excitability is exhibited. To this in many cases succeeds a rise of excitability, which is yet never of consequence and often scarcely recognisable. The increase of excitability during closure of the current is greatest at the negative pole. It rises along with the strength of the current up to a certain limit.

If the experiment is frequently repeated, the increase of the contractions remains about the same during each closure of the

current, even when the contractions called forth by the mechanical stimulus alone gradually fell off.

EXAMPLES.

Experiment 19.

$+P = 39$; $-P = 24{\cdot}5$; $E = 27$; 3 Meidinger, $Rh. = 760$; $\gamma = 27$.

The mechanical stimulus by itself occasions no contractions; the polarising current produces both make- and break-contractions. Under its influence very strong contractions take place, which remain at the same height all the time the current is closed, and disappear when it is opened.

Experiment 20.

$+P = 44$; $-P = 24$; $E = 26$; 3 Meidinger, $Rh. = 132$; $\gamma = 30$.

The mechanical stimulus causes small muscular contractions; the polarising current make- but not break-contractions. Directly after the current is closed the contractions produced by the mechanical stimulus become very powerful. They keep at nearly the same height all the time the current is closed; yet they do gradually fall, though the decrease is very trifling. When the current is opened they return to their initial magnitude; sometimes they rise beyond this. The diminution caused in the contractions is pretty much the same after repeated experiments, although the contractions produced by the mechanical stimulus alone gradually get weaker.

Experiment 21.

$+P = 44$; $-P = 26$; $E = 31$; $\gamma = 34$; 3 Meidinger.

The mechanical stimulus calls forth strong contractions. The strength of the polarising current is raised after each experiment. With $Rh. = 90$, the reinforcement of the contractions is still quite inconsiderable, though fully apparent. The stronger the current applied, the greater increase is there in the contractions as compared with those elicited by the mechanical stimulus alone. This increase of excitability is exhibited all the time the current is closed; the contractions occurring under its influence, however, slowly decline from the first one after closure, which is the strongest. After interruption of a current of low intensity they resume their former height, but with a certain strength of current ($Rh. = 450$) and upwards a lowering of excitability sets in directly after the current is opened, at first scarce recognisable, but always more clearly marked as the strength of the current increases. At the end of this diminution a moderate increase of excitability takes place.

Experiment 22. $+P = 30$; $-P = 16$; $E = 16$; $\gamma = 5$; 10 Meidinger, $Rh. = 20{,}000$; no paper under the nerve.

The mechanical stimulus produces excessively slight contractions; the constant current only make-contractions. Under its influence the contractions excited by the mechanical stimulus suddenly become of maximal intensity, one might even say tetanic; after interruption of the current they instantly vanish. In order to apply the mechanical stimulus quite close to the negative pole in this experiment as well as in the two following, I led the current to the nerve through a strip of filter-paper moistened with a 0·6 % solution of common salt.

Experiment 23. $+P = 30$; $-P = 12{\cdot}5$; $E = 13$; $\gamma = 12$; 10 Meidinger, $Rh. = 20{,}000$; no paper under the nerve.

The mechanical stimulus produces quite small contractions, the constant current make- and break-contractions. Under its influence the contractions evoked by the mechanical stimulus are very strong, almost tetanic. With interruption of the current they again decline, but are still a little greater than they previously were. The same action occurs if the current is once more closed.

Experiment 24. $+P = 33$; $-P = 14$; $E = 14$; 10 Meidinger, $Rh. = 20{,}000$; $\gamma = 5$.

The mechanical stimulus elicits weak contractions; the constant current only a make-contraction. Under the influence of the constant current the contractions produced by the mechanical stimulus reach maximal height, and retain this all the time the current is closed. After it is opened there appears first a diminution of the excitability, after which the contractions resume their original height.

9. The intrapolar changes of excitability at the positive pole of an ascending current.

The excitability of the nerve is lowered with all strengths of the current, even with the weakest. This diminution does not assume its full amount all at once, but the contractions fall off gradually under the influence of the current, so that the first contractions after contact is made, though considerably smaller than those preceding them, are somewhat greater than their successors. This lowered excitability lasts as long as the current is in action; yet it happens that the contractions meanwhile gradually increase, though the increase is only trifling and often does not occur at all. If the current is opened the contractions recur forthwith to

their previous height. No accompanying diminution of the excitability can be made out. On the contrary, in many cases an increase of the contractions sets in, which is yet never great, and occasionally is not at all noticeable. The greatest diminution during closure of the current takes place at the pole itself. It increases with the strength of the polarising current. If the experiment is repeated time after time, other conditions being the same, the diminution of excitability generally increases each time, though only to a very inconsiderable extent. The contractions elicited by the mechanical stimulus alone in most cases remain uniform throughout the experiment.

Examples.

Experiment 25. $+P = 39$; $-P = 24{\cdot}5$; $E = 36$; 3 Meidinger, $Rh. = 1000$; $\gamma = 27$.

The mechanical stimulus causes strong contractions, the polarising current make- and break-contractions. Immediately after contact is made the contractions sink to half their former height and remain thus as long as the nerve is traversed by the current. When the current is opened they regain their previous height. With repeated making and breaking of contact, the contractions produced under the influence of the polarising current decline gradually, whereas the mechanical stimulus by itself evokes contractions of tolerably uniform strength during the whole period.

Experiment 26. $+P = 44$; $-P = 24$; $E = 41$; 3 Meidinger, $Rh. = 132$; $\gamma = 33$.

a. The mechanical stimulus occasions moderately strong contractions; the polarising current make- but not break-contractions. Under its influence the contractions elicited by the mechanical stimulus disappear; the moment after closure, however, there is a trace of contraction. As soon as the current is opened the contractions exhibit their initial strength, with perhaps a slight increase.

b. $E = 39{\cdot}5$. Other conditions being the same, the nerve is stimulated somewhat farther from the pole. If a polarising current is applied of the same strength as in *a*, the muscular contractions fall off to a considerable extent, but not so much as in *a*. The first contraction after the current is thrown in is a trifle greater than its successors. Directly after the current ceases the contractions regain their original strength.

Experiment 27.

$+P = 34$; $-P = 16$; 3 Meidinger, $Rh. = 20$; $\gamma = 27$.

a. $E = 33$. The mechanical stimulus causes moderately strong contractions; the constant current neither make- nor break-contractions. Under its influence, however, the contractions become notably diminished, this decrease being less directly after the current is closed than afterwards. After interruption of the current the contractions return to their former strength and even go a little beyond.

b. $E = 30$. Under the influence of the same polarising current the diminution of excitability takes almost the same course as in *a*; the increase of diminution attending the continuance of the current is here quite clearly exhibited.

c. $E = 28{\cdot}5$. Here the diminution of excitability elicited by the same polarising current is considerably less than in *a* and *b*; all the circumstances attending it, however, make their appearance here just as much as in the foregoing series.

d. $E = 25{\cdot}5$. Here the polarising current causes a scarcely noticeable diminution of the contractions.

10. The change of position of the indifference-point with increasing strength of a descending current.

When I had convinced myself by means of the foregoing investigations that, up to the strongest polarising currents which were at my disposal, there was in the intrapolar tract a decrease of excitability at the positive, and an increase at the negative pole, it became important to examine in what way different strengths of current affected the relation between the length of the intrapolar portion of nerve exhibiting increased excitability, and that of the similar portion exhibiting decreased excitability; or, in other words, according to what law the indifference-point changed its position with varying strengths of the polarising current.

For this purpose I adopted the following procedure. I stimulated a given spot lying at a certain distance from the negative pole, and examined how the excitability there varied, when, beginning with quite weak currents, I progressively increased their strength. When I selected a spot not far from the negative pole, these contractions exhibited in the first place an increase, which became greater and greater the stronger the current used. When however its strength was still further raised, there showed itself instead a considerable diminution of the contractions. That this

did not depend on inhibition of excitation setting in at the negative pole itself was proved by the experiments given under 9, in which the nerve was stimulated directly at the negative pole, and where stronger currents were applied than in the case above mentioned.

With increasing strengths of the polarising current, therefore, the condition of diminished excitability extends over a correspondingly increasing extent of the intrapolar tract, and in the same proportion the part showing increased excitability decreases. In other words, as the strength of the polarising current increases, the indifference-point moves from the positive toward the negative pole.

With quite weak currents the condition of diminished excitability is exhibited only in the neighbourhood of the positive pole, while the greater part of the intrapolar tract shows increased excitability. With strong currents it is only in the immediate neighbourhood of the negative pole that an increased excitability can be demonstrated; a lowered excitability presents itself over all the rest of the intrapolar tract.

Examples.

Experiment 28. $+P = 44$; $-P = 23$; $E = 27$.

a. 2 Meidinger, *Rh.* = 19,360. The mechanical stimulus produces weak contractions; the constant current make- and break-contractions. Under the influence of the current the contractions evoked by the mechanical stimulus increase considerably, and when it is opened they return to their original size.

b. 4 Meidinger, *Rh.* = 19,360. The polarising current occasions make- and break-contractions; under its influence the contractions evoked by the mechanical stimulus show a persistent increase. When the current is interrupted a slight increase of the contractions sets in.

c. 6 Meidinger, *Rh.* = 19,360. The polarising current causes make- and break-contractions. Through its action the muscular contractions are completely arrested. Traces of them are visible only for a short time after the current is passed. On opening the current, however, the contractions are for a time greater than before.

d. 2 Meidinger, *Rh.* = 360. The polarising current produces make- and break-contractions. The mechanical stimulus, which was of the same strength all through the experiment, now excites no contractions, in consequence of exhaustion of the nerve. Under the influence of the polarising current, however, contractions still show themselves, though only slight ones.

Experiment 29. $+P = 30$; $-P = 13$; $E = 16$; $\gamma = 25$.

a. 3 Meidinger, *Rh.* = 360. The mechanical stimulus occasions weak muscular contractions; the constant current only make-contractions. Under its influence the contractions notably increase, and sink to their former size when the current is opened. Presently these quite disappear, but the contractions elicited under the influence of the current retain their original strength nearly unaltered.

b. $E = 15{\cdot}5$; 3 Meidinger, *Rh.* = 2,360. The nerve is stimulated at a spot only ·5 mm. distant from the preceding. The mechanical stimulus here causes rather weak contractions, the polarising current make- and break-contractions. Under its influence there follows a distinct increase of the contractions. After the current is shut off the contractions fall to their original amount.

c. $E = 16{\cdot}5$; 3 Meidinger, *Rh.* = 19,360. If the nerve is stimulated 1 mm. higher up than in *b*, and therefore ·5 mm. higher than in *a*, while the strength of the current is considerably raised, the latter now exerts an insignificant and indeed hardly perceptible influence in strengthening the contractions.

d. $E = 15{\cdot}7$; 6 Meidinger, *Rh.* = 19,360. The nerve is acted on by the stimulus at a spot in close proximity to that previously excited, and the strength of the current is so far raised as now to cause a make- contraction and only a small break-contraction. In this case the muscular contractions instantly disappear when the current is closed.

Experiment 30. $+P = 34$; $-P = 16$; $\gamma = 13$.

a. $E = 22$; 3 Meidinger, *Rh.* = 340. The mechanical stimulus produces rather weak muscular contractions, the constant current make- but no break-contractions. Under its influence the contractions elicited by the mechanical stimulus increase very considerably. When the current is opened they decline to their original height.

b. $E = 22$; 3 Meidinger, *Rh.* = 2,000. The polarising current brings about make- and break-contractions. Under its influence a very considerable increase occurs in the contractions produced by the mechanical stimulus, though by itself this calls forth only slight ones in consequence of exhaustion of the nerve.

c. $E = 22$; 3 Meidinger, *Rh.* = 20,000. With this greater strength of the polarising current the contractions increase still further than in *a* and *b*. When the current is opened there is a transitory rise in the height of the contractions as compared with that which they attained before contact was made.

d. $E = 21{\cdot}8$; 4 Meidinger, *Rh.* = 20,000. The nerve is stimulated ·2 mm. nearer the negative pole. The strength of the polarising current is considerably raised, but still produces both make- and break-contractions, though the latter are feebler than in *b* and *c*. Under the influence of the current the muscular contractions vanish instantaneously. With interruption of the current they recur, and then they exhibit a distinct but gradually declining rise as compared with their original height.

e. $E = 21{\cdot}8$; 4 Meidinger, *Rh.* = 1,880. With diminished strength of current, which, however, still produces both make- and break-contractions, there again occurs under the influence of the current a rise in the height of the muscular contractions.

These investigations have therefore sufficiently confirmed the results at which Pflüger arrived by means of electrical and chemical stimulation relative to the changes generated in nerve by a constant current. If a constant current is passing through an uninjured nerve the following laws hold good for all the modes of excitation at present available.

The excitability of the nerve is augmented at the negative pole, as well outside as inside, in whatever direction the current passes along the nerve.

The excitability of the nerve is diminished at the positive pole, as well outside as inside the pole, in whatever direction the current passes along the nerve.

At both poles the change of excitability, whether inside or outside, increases with the strength of the polarising current until, in consequence of that change, the muscular contraction has either attained its maximum or is completely annulled. Further changes in the excitability of the nerve can, of course, not be proved by an alteration in the magnitude of the muscular contractions.

It is at the two poles that the change of excitability is greatest, and from each of these it diminishes in both directions, i.e. both outwards and inwards.

At each pole the change of excitability extends outside the pole over tracts which are greater the stronger the polarising current.

In the intrapolar tract the indifference-point shifts from the neighbourhood of the positive pole towards the negative pole with increasing

strength of the polarising current and that quite independently of the direction in which the current flows along the nerve.

N.B. An exception to the above occurs in the case of the diminution and final cessation of the muscular contractions when with an ascending current the nerve is stimulated in the region of the negative pole. For the explanation of this phenomenon see further on.

How the change of excitability is developed during the first moments after contact is made, and in what manner it declines after interruption of the current, is more difficult to demonstrate than are the persistent changes of excitability of the nerve. The former changes are of a more fugitive nature than the latter, and for their demonstration special experimental arrangements are requisite. The proper aim of my investigation was not to enquire into this, but its chief object was to examine the persistent changes of excitability which establish themselves while the current is closed.

My investigations have, however, yielded results relating to the duration of the change which confirm those previously arrived at on this subject. Thus in general the following statements hold good as well for mechanical as for other kinds of stimulation processes, when the nerve is traversed by a constant current.

At the negative pole the change of excitability on closure appears immediately in its full strength.

At the positive pole the change of excitability on closure attains its maximum only by degrees.

At the negative pole, after interruption of the current, supposing the current not too weak, there is exhibited at first a diminution of excitability, which is afterwards followed by an increase.

At the positive pole, on opening, a rise of excitability occurs directly.

Here it should be observed that both the increase of excitability occurring at the negative pole after the current is opened, and the diminution of excitability perceptible there at the very first, *are not nearly so sharply marked with mechanical stimulation as with electrical, and often cannot be made out at all.*

The following statements hold good for the changes of excitability when the current is in action for several seconds.

At the negative pole in many cases the muscular contractions decline after having first reached a maximum. This decrease is for the most part exceedingly slight, and proceeds very slowly.

At the positive pole the muscular contractions in many cases rise from the minimum to which they had at first sunk, but this rise is exceedingly trifling and very slowly takes place.

These phenomena admit of but one explanation, namely, that the strength of the polarising current, when it has traversed the nerve for a certain time, is lowered by internal polarisation of the nerve[1]. When the change of excitability produced by the polarising current is so great that the excitation of the nerve becomes in consequence stronger than is required to evoke maximal contraction, or weaker than the minimal strength required to produce a response, the diminution in strength of the polarising current produced by polarisation is of course unobservable. Accordingly the phenomena in question are not always exhibited, only appearing when the excitation of the nerve resulting from the change of excitability has either not risen above the strength required to generate maximal contractions, or not fallen below the strength necessary to call forth minimal contraction.

These phenomena do not present themselves with very minute strengths of the polarising current, presumably because in that case the internal polarisation cannot rise to an observable degree.

Finally, the following statements hold good with respect to the repeated action of a polarising current passing constantly in the same direction along the nerve.

The muscular contractions originating at the negative pole remain for a long time at nearly the same height, even when, for other reasons, the contractions elicited by the test-stimulus would have fallen off.

The muscular contractions originating at the positive pole become gradually smaller, even when those produced by the test-stimulus alone remain throughout at nearly the same height.

In the foregoing exposition I have spoken of the increased and diminished excitability of the nerve in accordance with the faulty mode of expression in general use, instead of keeping closely to the actual results, and speaking of the occurrence under particular circumstances of an increase or decrease in the size of the muscular contractions.

If the view propounded by Hermann is right, the diminution or increase of the muscular contractions does not depend on a

[1] See du Bois-Reymond, Gesammelte Abhandlungen, II. p. 171.

local change of excitability in the nerve, but on the decrease or increase in strength of the excitation during its propagation along the nerve to the muscle.

It still remains then to examine whose theory, Pflüger's or Hermann's, best agrees with the facts, so far as they are at present known to us, relating to the changes in extent of the muscular contractions while a constant current is passing along the nerve.

In this connection special weight must be assigned to the above recorded experiments on the character of the muscular contractions when with an ascending current the nerve was stimulated close to the positive pole and inside it, and to those where with a descending current it was stimulated quite close to the negative pole.

These experiments have shown that, if the stimulus is made to operate near enough to the pole, the muscular contractions decrease in the former case under the influence of the polarising current, however weak it may be, and increase in the latter case however strong the polarising current.

According to Hermann's theory, the negative pole must be supposed to exert an inhibitory action on the propagation of the excitation, otherwise it could not explain the reason of the diminution and cessation of contraction when with a strong ascending current the nerve is stimulated above the negative pole. Here an experimentum crucis seems possible. If this phenomenon depends on inhibition, not at the positive, but at the negative pole, then plainly the effect of such inhibition should be to weaken and finally to annul the muscular contractions when the nerve is stimulated inside the pole with the current descending, provided that the intensity of the current is sufficiently great. This, however, is not the case. If with a descending current the nerve is stimulated sufficiently near the negative pole, the muscular contractions do not disappear, even when a polarising current of 10 Meidinger's elements is applied. They increase, on the contrary, and this to such a degree, that a strength of stimulus which before closure evoked no contractions at all, is now, under the influence of the current, able to evoke maximal contractions.

Not only therefore does the negative pole exert no inhibitory action on the propagation of a stimulus to the muscle, but, quite the reverse, the excitability of the nerve is very considerably increased.

On the other hand, a much smaller strength of current is sufficient

completely to arrest the action of the stimulus when exercised in the region of the positive pole.

Hermann's theory, therefore, cannot explain all the phenomena which attend the changes produced by a constant current in the magnitude of the muscular contractions. They may, however, be explained by Pflüger's theoretical view in accordance with which the cause of the changes in size of the muscular contractions is to be sought *in the local changes of excitability produced by the current in the nerve.* Until new facts are discovered which necessitate a modification of this view, it may be accepted.

No such fact has presented itself in the foregoing investigation.

II.

CONTRIBUTION TO THE THEORY OF THE BREAK-CONTRACTION.

By Dr. ROBERT TIGERSTEDT.

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II.

THROUGH the indefatigable labours of du Bois-Reymond, of Pflüger, and of several other observers, abundant material has been accumulated, consisting of carefully-ascertained facts relative to the exciting action of the electric current on nerves. These facts may be summed up very briefly in the following propositions. (1) It is not to the absolute value of the current density at any moment that the motor nerve responds by contraction of its muscle, but to the change of this value from one moment to the next, in such sense that the excitation to movement following these changes is the more considerable, the more rapidly they have proceeded when of equal amount, or the greater their amount in a unit of time (Law of du Bois-Reymond[1]). (2) When the current is closed, it excites at its negative pole; when it is opened, the nerve is stimulated at the positive pole[2]. (3) While the current is closed, the excitability of the nerve is weakened in the neighbourhood of the positive pole, strengthened in the neighbourhood of the negative pole[2]. (4) In the first moments after opening of the current, the excitability of the nerve is strengthened at the positive pole, and weakened at the negative pole[2]. The greater part of these facts Pflüger summed up in his well-known principle, '*A given tract of nerve is stimulated by the appearance of katelectrotonus and the disappearance of anelectrotonus, not however by the disappearance of katelectrotonus nor by the appearance of anelectrotonus*[3].' He further

[1] Du Bois-Reymond, Untersuchungen über thierische Elektricität, Berlin, 1848, pp. 258–259. (The original paper appeared in 1845.)

[2] Pflüger, Untersuchungen über die Physiologie des Electrotonus, Berlin, 1859; v. Bezold, Untersuchungen über die electrische Erregung der Nerven und Muskeln, Leipzig, 1861.

[3] Pflüger, *loc. cit.* p. 456.

showed that from this principle the law of contraction as he had found it could be deduced with the greatest ease.

The fact, that when the current is closed, excitation occurs at the negative pole, connects itself with a number of purely physical phenomena. Thus, for example, in the induction spark the electric light shows itself only at the negative pole. In vacuo, the negative pole is entirely surrounded with a beautiful violet light, while the positive pole emits only a luminous crown of purple-coloured rays. The temperature of the violet is higher than that of the purple light. In the voltaic arc the light constantly appears first at the negative pole, while the positive is yet dark; presently this too gets warmed up, small particles begin to pass over, and so on (Neef, Ruhmkorff, Despretz, Moigno[1]).

We have therefore analogies derived from other sources, which teach that, at least in some cases, the electric current acts most powerfully at the negative pole. There are also facts which might serve as analogies for the changes of excitability occurring at both poles during the closure of a current. Thus Matteucci[2], and after him Fleischl[3], found that, when nerves are treated with weak alkaline solutions (·08 %), their excitability rises, and that, on treatment with weak acids (·075 %), it falls. Now we know that the current gives off acids at its positive pole and alkalies at its negative. We have here, therefore, a complete agreement between the changes of excitability elicited by the constant current and those generated by the corresponding electrolytes. To these facts we may add an old observation of Gustav Crusell's, who found that the organic tissues are coagulated at the positive pole, probably through the formation of acids, and that the coagulum formed is again liquefied by the negative pole, probably through the alkalies liberated there, or in other words, the positive pole makes the structure of organic tissues firmer, while the negative pole exerts the contrary action[4].

[1] Daguin, Traité élémentaire de Physique, iii, Paris and Toulouse, 1879, pp. 472–473.

[2] Matteucci, Comptes Rendus de l'Académie des Sciences, tom. 65, p. 155, 1867.

[3] Fleischl, Archiv f. Anatomie und Physiologie, 1882, p. 17.

[4] G. Crusell, Über den Galvanismus als chemisches Heilmittel gegen örtliche Krankheiten, St. Petersburg, 1841, p. 14 et seq.

Among Crusell's experiments the following may be given here: 'If a galvanic current from a small compound battery is led into the eye of a living animal by means of a needle introduced through the cornea, after the current has been in operation half a minute, a whole minute, or longer, according to the strength of the battery, there occurs, often at once, at latest after some days, a clouding of the pupil, sometimes associated with a partial coagulation of the aqueous humour. If the galvanic

Analogy, however, does not necessarily imply identity. Though we may point to phenomena in other provinces similar to those with which we have become acquainted in studying the action of the current on nerves, we cannot regard the two as equivalent; nor form by their aid any sufficient and complete theory of the phenomena which occur at the moment that the current is closed and during the period of its flow along a nerve. Yet these analogies and others of a like kind are perhaps not without value, since at any rate they suggest a possibility, however slight, of getting beyond the bare facts of experiment.

It is quite otherwise with the break-excitation and with the other phenomena attending opening of the current. We can, so far as I know, point to no similar facts in other provinces of knowledge, and Pflüger's famous formula, that the disappearance of anelectrotonus stimulates, is merely a very precise and exact wording of the facts. It states, however, nothing more, and advances us not one step towards understanding the essence of the phenomenon. Even at the earliest period in the history of electrophysiology, the break-contraction had arrested the attention of enquirers; and even Volta attempted to find for it a theoretical explanation. Neither he nor his followers, however, succeeded in presenting a theory which satisfied the requirements of science; and his views, as well as those of Pfaff, Lehot, Erman, Marianini, and the earlier ones of Matteucci, can now claim merely an historical interest[1].

Peltier, whose views appear to be more important than these, explains the break-contraction in direct contraction as due to the polarisation of the muscle, expressing himself thus: 'On doit à M. Ritter'—he says—'puis à M. De La Rive la connaissance de ce fait; qu'un arc métallique, formant un circuit hydroélectrique par

current is led *from* the eye in the same way, there occurs at once a copious disengagement of gaseous bubbles, and, if the eye has been previously exposed to the action of the in-going current, there occurs usually a manifest diminution of the clouding and of the coagulum, both of which nearly disappear in a few weeks, especially if the experiment is accompanied with only a slight amount of inflammation' (pp. 11–19).

I repeated the experiment in the following way. I used a battery of 5 or 6 Meidinger's elements. When I applied the positive pole to the cornea of a frog which had just been killed, and the negative to any part of the trunk, after a few moments there appeared a distinct clouding of the cornea. When I changed the direction of the current, so that the negative pole rested on the cornea, there was at once a copious disengagement of minute bubbles of gas; these being removed, the cornea appeared almost as clear and transparent as at first.

[1] See the complete account by du Bois-Reymond, Untersuchungen über thierische Elektricität, Berlin, 1848, pp. 307–402.

son immersion dans deux liquides séparés, devient un couple voltaïque et produit un courant en sens inverse d'autant plus énergique que le metal est plus inaltérable. On avait pensé d'abord qu'une polarisation moléculaire de tout l'arc était la cause de ce contre-courant; mais il a été reconnu depuis qu'il n'y avait que les bouts immergés qui jouissaient de cette faculté, et qu'elle était due à une couche d'oxigène au pôle positif, et une d'hydrogène au pôle négatif. La même cause produit les mêmes effets sur la grenouille; la patte positive se charge d'oxigène, et la negative d'hydrogène. Le contre-courant se démontre en plongeant les pattes dans deux tasses ou aboutit le fil d'un galvanomètre très-sensible. . . . Plus la pile sera forte, plus le temps du courant sera long, plus les pattes seront chargées. . . . Ce qui est vrai pour une grenouille entière l'est encore pour un muscle, pour une portion de muscle,' &c. [1]

Du Bois-Reymond, who established the correctness of Peltier's facts by investigations of his own [2], urged against his explanation of the break-contraction that it was not easy to see how it could be thus explained, since these electrical charges of Peltier would seem to require a complete circuit to produce a current, a condition lost in the very act of interruption [3]. It may however be said, in answer to this objection of du Bois-Reymond, that the equalisation of the differences of tension which exist in the muscle at the moment when the external circuit is broken gives rise to internal currents.

All this holds only for the break-contraction elicited by direct excitation of the muscle, but may however be applied to the break-contraction resulting from stimulation of the nerve, as to all appearance it is identical with the other.

Peltier's view was taken up by Matteucci, but carried no further. He contented himself with pointing out that the break-contraction

[1] 'We owe to M. Ritter,' he says, 'and after him to M. De La Rive, the knowledge of this fact, that a metallic arc, forming a hydroelectric circuit by its immersion in two separate liquids, becomes a voltaic couple and produces a current in the reverse direction, which is the more energetic the more unalterable the metal. It was at first thought that a molecular polarisation of the whole arc was the cause of this counter-current; but it has since been recognised that it is only the immersed ends which possess this property, which is due to a layer of oxygen at the positive pole and to one of hydrogen at the negative pole. The same cause produces the same effect in the frog; the positive foot gets charged with oxygen, the negative with hydrogen. The reverse current shows itself when the feet are plunged into two cups, in which the wires of a very sensitive galvanometer terminate. . . . . The stronger the battery and the longer the duration of the current, the more highly charged the feet become. . . . . What is true of a whole frog is true of a muscle, of part of a muscle,' &c.

[2] Du Bois-Reymond, *loc. cit.* i. pp. 377–382.

[3] Ibid. *loc. cit.* p. 381.

could be explained by the susceptibility of the nerve to internal polarisation, without making the slightest attempt to show how all the phenomena characterising and attending the break-contraction could be deduced from it[1].

Moreover, the internal polarisability of nerves had not been studied sufficiently to admit of a true parallel being drawn between it and the break-contraction. It is easy to explain, therefore, why this statement has received no further attention from physiologists.

Then came Pflüger's investigations, which have to so great an extent impressed the nerve physiology of to-day. Pflüger's conception of the break-contraction has since then been accepted almost without objection, although, as already explained, it supplies no explanation of the phenomena, but only an elegant statement of their laws.

A remarkable theory was put forward about the same time by Chauveau. According to him the physiological action of electricity is 'the result of a mechanical disturbance communicated to the molecules placed in the path of the current[2].'

The constant current in general excites only by means of 'an accessory instantaneous current of high tension, with which it commences;' and similarly by means of 'an accessory instantaneous current of high tension, with which it terminates[3].' Of these currents the first flows in the same direction as the stimulation-current, and the second in the opposite direction. The action of the last is assisted by the polarisation-current[4].

In later times, so far as I know, only H. Munk has attempted to advance a real theory of the break-contraction. His theoretical view starts from the phenomenon of Porret, and is thus presented by the author himself: 'The excitation of the nerve is due in the first place to the direct displacement of the nerve fluid in the direction of the current, and similarly, by the return of the fluid, when the current is opened, to those parts of the nerve whence it had come. Inasmuch as these movements of the nerve-fluid extend over the extrapolar tract to the muscle, the muscular contraction is produced by the motion of the nerve-fluid—independently of its direction—provided that the motion is propagated to the muscle with sufficient intensity and velocity[5].'

Munk therefore would regard both the make- and the break-contraction as caused by a mechanical excitation. It is, however,

[1] Matteucci, Comptes Rendus, tom. 65, 1867.
[2] Chauveau, Journal de la Physiologie, iii. No. ix. p. 52, January, 1860.
[3] Ibid. *loc. cit.* pp. 61–66. [4] Ibid. *loc. cit.* p. 70.
[5] H. Munk, Archiv für Anatomie, Physiologie, &c., 1866, p. 383.

impossible to conceive that the displacing power of a very weak current, such as is just able to produce a muscular contraction, would be sufficiently great and could occur with sufficient suddenness to exert such an action. Moreover, the facts made out by Munk in this connection relative to the changes of excitability produced by a constant current, which were to have supported his conception, do not agree with the results of foregoing and succeeding investigations. Besides, he has never published the complete account of his theory. We need therefore give it no further consideration.

II.

Certain phenomena, which I observed in the course of my investigations upon the changes of excitability produced in nerves by the constant current, led me to enquire whether the internal polarisation of nerves might not be the true cause of the break-contraction. Accordingly, I devoted myself in the first place to a thorough investigation of the internal polarisation of nerves, and soon found that it afforded in a remarkable degree the conditions required for the production of a break-contraction.

The chief laws of the internal polarisation of nerves are these :—

1. With a current whose strength is not greater than that produced by three Meidinger's elements polarisation is, as near as may be, directly proportional to the strength of the current.

2. If the polarising current acts on the nerve for unequal and increasing lengths of time, other conditions being the same, polarisation increases; it rises more rapidly at first, and afterwards more slowly, finally approaching its maximum with extreme slowness.

3. When the polarising current is opened, polarisation instantly attains its highest value, and after this declines continuously. This decline proceeds at first very rapidly, afterwards however more and more slowly, so that polarisation is still present for a long time after the opening of the polarising current, and approaches the zero point only asymptotically.

The two chief conditions on which the strength of polarisation depends are identical with those which determine the break-contraction, as to which it has long been known that it is in the main a function of the strength and duration of the polarising current. But the third law of polarisation also tells in the occurrence of the break-contraction in a very remarkable way. Since polarisation lasts for an appreciable time after interruption of the polarising current, the break-contraction, if it has once occurred

on application of a strong current A, must also occur with a weaker current B, if only this current is closed soon enough after the stronger current is opened. For, to the polarisation produced by the current B, which of itself is not sufficient to cause a break-contraction, there is added the polarisation remaining over from the current A, and the sum may now be strong enough to liberate a contraction. Further, under such circumstances, the break-contraction must the more certainly appear, and must be the greater in extent the sooner the current B is closed after the opening of A.

These phenomena are very easily observed in excitation experiments. The description of them by Biedermann is in accordance with the preceding considerations. He found in fact that '*directly after a break-contraction liberated by a strong current, weak currents, previously only effective at make, exercise an excitatory action at break which is almost as intense as that of the strong current. This excitation-effect diminishes, however, in a short time, and disappears completely after a few minutes of rest if the nerve is sufficiently vigorous. Moreover, under conditions otherwise the same, this peculiar effect is the more persistent the greater the period of time during which the stronger current has operated, and the less active the nerve is*[1].'

The full parallelism between the break-contraction and polarisation may be very elegantly demonstrated with one and the same strength of current on an ordinary nerve-muscle preparation. I performed such experiments in this way. I passed a current of a given strength through the nerve for periods of various duration. If the period was very short, only a make-contraction occurred; if it was longer, there was also a break-contraction. If, directly after the break-contraction appeared, I again closed the current and opened it again very soon, repeating the experiment in this way for several successive times, I obtained a whole series of break-contractions, which by-and-bye fell off in size, and at last quite ceased, to reappear as soon as I allowed the current to act on the nerve for a longer time. In these experiments therefore there appeared in the break-contractions all the phenomena which I had previously become acquainted with by means of the galvanometer. In order to throw more light on the question I shall here communicate some examples of experiments.

In the following records, T^1 = the duration of the closures;

[1] Biedermann, Wiener Sitzungsberichte Math. Part iii. vol. 83, p. 328, 1881.

T^2 = the intervals during which the current remained open; C = the size of the break-contraction.

The muscle traced its contractions by means of a spring lever on the cylinder of Marcy's registering apparatus, which moved with the greatest regularity. They were magnified about 3·5 times. The electrodes used were, of course, unpolarisable.

Experiment I.—2 Meidingers, 500 rheochord-units in the derivation circuit; current ascending.

No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.
	"	"	"		"	"	"		"	"	"
1	0·5		0	9	6·4		3·5	17	0·4		0
		0·4				0·8				0·5	
2	0·4		0	10	1·0		2·1	18	1·9		0
		0·5				0·7				0·7	
3	0·4		0	11	0·6		2·2	19	5·0		2·9
		0·4				0·6				0·7	
4	0·4		0	12	0·5		2·0	20	0·6		2·9
		0·4				0·6				0·6	
5	1·8		0	13	0·5		0	21	0·5		0
		0·7				0·6				0·5	
6	3·5		0	14	0·5		0	22	0·5		0
		0·7				0·6				0·5	
7	3		0	15	0·5		0	23	0·5		0
		0·6				0·5				0·5	
8	5·4		0	16	0·4		0	24	7·2		5·5
		0·7				0·5					

Experiment II.—2 Meidingers, rheochord 800; ascending current.

The † under column C denotes that . . . . is just noticeable.

No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.
	"	"	"		"	"	"		"	"	"
1	0·3		0	14	0·3		1·2	27	0·5		2·6
		0·3				0·4				0·5	
2	0·2		0	15	0·3		2·2	28	0·4		1·9
		0·3				0·4				0·5	
3	0·2		0	16	0·2		1·1	29	0·3		1·9
		0·3				3·0				0·5	
4	0·2		0	17	0·2		0	30	0·3		2·2
		0·3				0·6				0·5	
5	0·2		0	18	0·2		0	31	0·2		1·8
		0·3				0·6				0·5	
6	0·2		0	19	0·3		0	32	0·3		0·5
		0·3				0·6				0·4	
7	1·6		†	20	0·2		0	33	0·2		0·5
		0·6				0·6				0·5	
8	5·1		2·8	21	0·2		0	34	0·2		†
		0·7				0·6				0·5	
9	0·5		2	22	0·2		0	35	0·2		†
		0·5				0·6				0·5	
10	0·4		2·6	23	1·7		0	36	0·2		0·9
		0·5				0·7				2·5	
11	0·3		2·3	24	3·9		2·3	37	0·1		0
		0·4				0·6				0·9	
12	0·3		1·8	25	0·4		1·8	38	0·3		0·9
		0·4				0·5				4·4	
13	0·3		1·5	26	0·4		1·5	39	0·2		0·9
		0·4				0·5				0·8	

No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.
	"	"	"		"	"	"		"	"	"
40	0·3		0	43	0·3		0·7	46	1·6		1·0
		0·5				0·4				0·7	
41	0·4		0	44	0·3		†	47	0·9		1·0
		0·5				0·4					
42	0·3		†	45	0·3		0				
		0·4				0·4					

Experiment III.—2 Meidingers, rheochord 500; ascending current.

The † under column *C* denotes that . . . . is just noticeable.

No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.
	"	"	"		"	"	"		"	"	"
1	0·3		0	12	0·2		†	23	0·2		0·5
		0·5				0·5				0·4	
2	0·3		0	13	0·2		†	24	0·2		0·4
		0·5				0·4				0·4	
3	0·2		0	14	0·2		0	25	0·2		0·5
		0·5				0·5				0·4	
4	0·2		0	15	0·2		†	26	0·2		†
		0·5				0·5				0·4	
5	1·9		†	16	0·2		0	27	0·2		0
		0·8				0·4				0·4	
6	6·8		1·8	17	0·2		0	28	0·2		0
		0·6				0·5				0·4	
7	0·3		∪	18	0·2		0	29	0·2		†
		0·5				0·5				0·4	
8	0·2		0	19	0·2		0	30	0·2		0
		0·5				0·5				0·4	
9	0·2		0	20	11·6		7·1	31	0·2		0
		0·6				0·6				0·4	
10	14·9		5·0	21	0·3		2·7	32	0·2		0
		0·8				0·4				0·4	
11	0·3		1·5	22	0·2		0·9	33	0·2		0
		0·6				0·4					

Experiment IV.—2 Meidingers, rheochord 1000; ascending current.

The † under column *C* denotes that . . . . is just noticeable.

No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.	No.	T^1.	T^2.	C.
	"	"	"		"	"	"		"	"	"
1	0·4		0	12	0·2		1·0	23	0·3		†
		0·4				0·4				0·5	
2	0·4		0	13	0·2		†	24	0·2		†
		0·4				0·4				0·5	
3	0·3		0	14	0·2		†	25	0·2		†
		0·4				0·4				0·5	
4	0·3		0	15	0·3		†	26	1·1		†
		0·4				0·4				0·8	
5	0·3		0	16	0·2		†	27	0·7		†
		0·4				0·4				0·8	
6	0·3		0	17	2·7		2·2	28	1·0		1·1
		0·4				0·7				0·8	
7	0·3		0	18	0·6		1·4	29	13·2		5·4
		0·4				0·6				0·7	
8	0·3		∪	19	0·5		1·3	30	0·2		1·6
		0·4				0·4				0·4	
9	3·4		1·0	20	0·5		0·6	31	0·2		1·1
		0·8				0·6				0·3	
10	10·9		2·6	21	0·6		1·1	32	0·2		†
		0·6				0·5				0·3	
11	0·3		1·0	22	0·5		0·8	33	0·1		†
		0·4				0·5					

Experiment V.—2 Meidingers, rheochord 1970; ascending current.

The † under column *C* denotes that . . . . is just noticeable.

No.	T^1.	T^2.	*C.*	*No.*	T^1.	T^2.	*C.*	*No.*	T^1.	T^2.	*C.*
	"	"	"		"	"	"		"	"	"
1	0·4		0	12	0·3		0	23	0·3		†
		0·5				0·4				0·4	
2	0·3		0	13	0·3		0	24	0·3		1·0
		0·5				0·4				0·4	
3	0·3		0	14	0·3		0	25	0·3		1·0
		0·5				0·4				0·5	
4	1·4		0	15	8·3		3·4	26	0·3		1·4
		0·8				0·9				0·4	
5	3·2		1·8	16	0·5		5·1	27	0·3		0
		1·0				0·5				0·4	
6	1·0		2·2	17	0·4		3·2	28	0·3		†
		0·7				0·5				0·5	
7	0·3		2·2	18	0·4		2·8	29	0·2		†
		0·7				0·5				0·5	
8	0·4		1·3	19	0·4		1·6	30	0·2		†
		4·7				0·5				0·5	
9	0·3		0	20	0·3		1·4	31	0·2		†
		0·5				0·5				0·5	
10	0·3		0	21	0·3		1·4	32	0·2		1·7
		0·5				0·4				0·5	
11	0·3		0	22	0·3		1·3	33	0·2		†
		0·4				0·4				0·5	
								34	0·2		†

We have thus seen that, as regards the fundamental phenomena, there is a complete parallel between polarisation and the break-contraction. But characteristics of secondary importance also show remarkable agreement.

Biedermann[1] found that when nerves are treated with an alcoholic solution of common salt, not only was the break-contraction stronger, but also that it made its appearance with a strength of current which before was quite inadequate to produce it. I also have found that, when the nerve is treated with an alcoholic solution of common salt, its susceptibility to polarisation is increased by half, as the following experiments show. They were conducted after precisely the same method as my earlier experiments on internal polarisation. I used a 0·6 % solution of common salt mixed with 10 % of alcohol, and took the greatest care that the contact should be the same both before and after the treatment with alcohol.

[1] Biedermann, *loc. cit.* p. 321. The retardation of the break-contraction discovered by Biedermann at the same time does not for the present concern us.

Experiment VI.—3 Meidingers, rheochord 1000; duration of closure 5″; distance between the electrodes 8mm.

1. Before application of the alcohol:—

No.	*Deflection.*
1	2·8
2	2·95
3	3
4	2·95
5	3
Mean	2·94

Mean variation 0·064.

2. After application of the alcohol for 1 minute:—

No.	*Deflection.*
6	3·8
7	4·4
8	4·35
9	4·45
10	4·2
Mean	4·24

Mean variation 0·192.

Experiment VII.—3 Meidingers, rheochord 1000; duration of closure 5″; distance between the electrodes 20mm.

1. Before application of the alcohol:—

No.	*Deflection.*
1	3·1
2	3·2
3	3·1
4	3·2
5	3·4
Mean	3·2

Mean variation 0·08.

2. After application of the alcohol for 1 minute:—

No.	*Deflection.*
6	4·8
7	4·9
8	5·0
9	4·7
10	5·0
Mean	4·88

Mean variation 0·094.

Experiment VIII.—3 Meidingers, rheochord 1000; duration of closure 5″; distance between the electrodes 8mm.

1. Before application of the alcohol:—

No.	*Deflection.*
1	5·2
2	5·2
3	5·2
4	4·9
5	4·7
Mean	5·08

Mean variation 0·144.

2. After application of the alcohol:—

No.	*Deflection.*
6	7·2
7	6·7
8	6·8
9	6·8
10	6·6
Mean	6·82

Mean variation 0·152.

Here, again, the changes in polarisability are parallel with the occurrence of break-contractions. The same phenomena that Biedermann observed in the muscular contractions after treatment of the nerve with alcohol present themselves when we examine with the galvanometer the polarisation of the nerve.

In a paper which well deserves attention Grützner has recently considered, amongst other questions, the occurrence of the break-contraction when different parts of a nerve are stimulated[1]. We shall, for the present, pass over Grützner's conclusions relative to the significance of the 'nerve current' in the production of the break-contraction, and only note that in his experiments, when the plexus was stimulated, the break-contraction occurred as well with an ascending as with a descending current, if the slider of his rheochord (he employed a rheochord with one wire, of the same construction as that used for compensation experiments) stood at from 80 to 140mm from the zero point. If, however, the nerve was stimulated in the middle, below where the branches to the thigh are given off, above its separation into the two end divisions, and in the same way if it was stimulated near the knee, in most cases

both make- and break-contractions failed to appear even when the slider stood at 1000^{mm} from the zero point[1].

If the break-contraction is determined by a polarisation of the nerve, then, ceteris paribus, the susceptibility of the plexus to polarisation must be greater than that of the lower tracts of the nerve.

And this is actually the case. In experiments on this question the two sciatics of one and the same frog were fastened together, and different tracts of the nerve submitted to the polarising current. As the same electrodes and the same parts of them were used in all the experiments, and as at the same time the distance between them was constant, it is clear that the differences in the extent of the deflections, which were produced when different parts of the nerve were experimented on, are entirely dependent on local conditions. In other words, the polarisability of a nerve differs at different points of its course. What this depends on does not affect the question before us, which is whether any parallelism exists between polarisability and Grützner's results. I proceed to give some examples of experiments. I examined the polarisation of each nerve preparation at three different places, namely, (1) at the plexus, (2) where the branches to the thigh were given off, (3) in the lowest part of the nerve.

Experiment IX.—3 Meidingers, rheochord 1000; duration of closure 5″; distance between the electrodes 8^{mm}.

I.

No.	*Deflection.*
1	2·6
2	2·95
3	3·0
4	2·95
5	3·0
Mean	2·94

Mean variation 0·056.

II.

No.	*Deflection.*
6	1·1
7	1·0
8	1·25
9	1·25
10	1·20
Mean	1·16

Mean variation 0·088.

[1] Grützner, *loc. cit.* pp. 163–165.

III.

No.	*Deflection.*
11	1·05
12	1·15
13	1·0
14	1·0
15	1·1
Mean	1·06

Mean variation 0·052.

Experiment X.—3 Meidingers, rheochord 1000; duration of closure 5″; distance between the electrodes 10^{mm}.

I.

No.	*Deflection.*
1	4·8
2	5·3
3	5·25
4	5·1
5	5·15
Mean	5·12

Mean variation 0·136.

II.

No.	*Deflection.*
6	3·1
7	3·3
8	3·25
9	3·2
10	3·4
Mean	3·25

Mean variation 0·08.

III.

No.	*Deflection.*
11	1·15
12	1·40
13	1·35
14	1·40
15	1·35
Mean	1·33

Mean variation 0·072.

Experiment XI.—3 Meidingers, rheochord 1000; duration of closure 5″; distance between the electrodes 10^{mm}.

I.

No.	*Deflection.*
1	4·7
2	4·9
3	4·9
4	4·9
5	5·0
Mean	4·88

Mean variation 0·072.

II.

No.	*Deflection.*
6	3·45
7	3·7
8	4·0
9	3·65
10	3·8
Mean	3·72

Mean variation 0·144.

III.

No.	*Deflection.*
11	2·1
12	2·15
13	2·1
14	2·1
15	2·15
Mean	2·12

Mean variation 0·024.

Experiment XII.—3 Meidingers, rheochord 1000; duration of closure 5″.

I.

No.	*Deflection.*
1	4·35
2	4·35
3	4·35
4	4·2
5	4·2
Mean	4·29

Mean variation 0·072.

II.

No.	*Deflection.*
6	2·4
7	2·25
8	2·5
9	2·5
10	2·4
Mean	2·41

Mean variation 0·072.

III.

No.	*Deflection.*
11	1·3
12	1·45
13	1·50
14	1·75
15	1·75
Mean	1·55

Mean variation 0·160.

These experiments may suffice to show the agreement between Grützner's results and the polarisability of different tracts of the nerve. On what this difference of polarisability depends does not, as I have already pointed out, concern the question with which we are now occupied. It is probably due, mainly at least, to the greater conductivity of the thicker parts of the nerve. I have not attempted to determine whether other circumstances also exert an important influence.

We have found, therefore, a most remarkable parallelism between the break-contraction and polarisation, not merely in the fundamental phenomena, but also in those of secondary importance. I may therefore venture to regard polarisation as the cause of the break-contraction, *which, accordingly, is neither less nor more than a make-contraction dependent on the existence of a polarisation current.*

It is self-evident that the absolute magnitude of the polarisation-current cannot be regarded as an objection to this theory. The exciting action of a current is conditional, not on its strength alone, but also on the abruptness of its commencement. It is for this reason, for example, that the effect of an induction-shock on the nerve is so much greater than that of the constant current. The current of polarisation, already in existence during the passage of the polarising current, must come into action when the latter is opened, with an abruptness almost equal to that of an induction-shock, and so produce an excitation in spite of the smallness of its absolute strength. From this quarter, therefore, so far as I can see, no objection can be made to my theory. When the circuit of the polarising current is broken, that of the polarisation current is closed through the physiologically inactive nerve-sheaths, independently of any external derivation. In order to test still further this theoretical view, as well as its working capabilities, I shall now enquire whether we can obtain a simple and unstrained explanation of all the well-established phenomena presenting themselves on interruption of the polarising current.

III.

The fundamental conception in my theory of the break-contraction is the reference of all the phenomena appearing on interruption of a current to those which are exhibited on its closure. This once made good, it then only remains to explain scientifically the make-contraction and its attendant phenomena, to enable us to construct a satisfactory theory of the action of the electric current on nerve.

In short, we have now to examine whether, in reality, all the facts we find when the current is broken are really in accordance with those which present themselves when it is closed.

Just as the polarising current produces its exciting effect on closure at the negative pole, so the seat of stimulation at break is at the positive pole, which now becomes the negative pole of the polarisation-current.

And, just as the positive pole of the polarising current exerts a blocking action, so at break there is a tendency to blocking at the negative pole, for this is now the positive pole of the polarisation-current. Starting from this, we can with the greatest ease establish theoretically the law of contraction.

Most physiologists of the present day are agreed in expressing the law of contraction in its most general form after Pflüger's well-known scheme.

LAW OF CONTRACTION[1].

Strength of current.		*Ascending current.*	*Descending current.*
Weak current	Make:—	Contraction	Contraction
	Break:—	Rest	Rest
Moderate current	Make:—	Contraction	Contraction
	Break:—	Contraction	Contraction
Strong current	Make:—	Rest	Contraction
	Break:—	Contraction	Weak contraction or rest

If my interpretation of the make-contraction is correct, the same phenomena must occur when a descending current is broken as when an ascending current is closed, and, conversely, we shall encounter the same phenomena when an ascending current is broken as when a descending current is closed. The first stage of Pflüger's law will be the only exception, as the current has not yet attained the intensity required to produce polarisation of sufficient strength. The following scheme offers a survey of these relations, the first stage being omitted for reasons already given.

[1] Pflüger, Untersuchungen über die Physiologie des Electrotonus, Berlin, 1859, p. 454.

I.

Strength of current.	*Break of a descending current.*	*Make of an ascending current.*
Moderate current	Contraction	Contraction
Strong current	Rest or weak contraction	Rest

II.

Strength of current.	*Break of an ascending current.*	*Make of a descending current.*
Moderate current	Contraction	Contraction
Strong current	Contraction	Contraction

We see, therefore, that the agreement is as complete as the theory requires.

In order now to deduce the law of contraction from my standpoint, I assume that the relation between the strength of stimulation and the tendency to blocking is quite the same in the polarisation-current as in other currents; and that therefore, according to Pflüger's view, with a certain strength of this current, the stimulation overpowers the tendency to blocking, while with a greater strength the latter may become sufficiently great to prevent the excitation from reaching the muscle notwithstanding its greater strength.

The currents described as weak in Pflüger's law of contraction are, therefore, naturally those which are not strong enough to evoke a sufficient degree of polarisation in the nerve, and which are consequently unaccompanied by a break-contraction.

If the strength of the polarising current is above this limit, then on breaking a polarisation-current is produced of sufficient intensity to liberate a muscular contraction. It is true that when the polarising current is descending the excitation produced by the polarisation-current has of course to pass its own positive pole, which exerts a blocking action. This blocking action, however, is

as yet too weak to prevent the excitation being propagated to the muscle, just as with an ascending polarising current of weak or moderate strength the closing excitation at the negative pole is not prevented from reaching the muscle.

Strong currents are characterised by this, that the blocking which takes place at the positive pole overpowers the excitation proceeding from the negative pole. When the current is descending this is of no consequence; but if, on the other hand, the current is ascending, the blocking at the positive pole is sufficient to stop the excitation occurring at the negative pole.

If the polarising current is ascending, the polarisation-current is descending. However strong it may be made by strengthening the polarising current, it must always evoke a contraction, since there is nothing to hinder the excitation occurring at its negative pole from being propagated to the muscle.

It is otherwise if the polarising current is descending. In that case the polarisation-current is ascending, and the excitation has to pass the positive pole. The stronger the polarising current is, the stronger also do the polarisation-current and the block at its positive pole become. Yet, in order completely to prevent the excitation from reaching the muscle, the strength of polarisation must be considerable. Experience, moreover, teaches that the descending break-contraction is far from disappearing with a strength of current which is sufficient completely to do away with the ascending make-contraction. It may even happen, as Pflüger expressly stated in his original scheme of the law of contraction, that the descending break-contraction does not disappear at all. The reason, of course, is that the polarisation-current is not sufficiently strong.

The polarisation remaining over from previous stimulations has also in all likelihood much to do with the disappearance of the descending break-contraction. In experiments on Pflüger's law of contraction, as is well-known, we soon find that the ascending make-contraction disappears. It only remains then to bring about the disappearance of the descending break-contraction to demonstrate the whole law. If we now gradually increase the strength of the polarising current, we need no longer keep changing its direction, but may content ourselves with testing its action when descending, since we have already become acquainted with the whole law of contraction so far as concerns an ascending current. Every such stimulation, however, with a descending current leaves behind it a

polarisation-current flowing in the opposite direction; the sum of all these residual polarisation-currents make in the end a polarisation-current sufficiently strong to block the descending break-excitation.

My theory explains therefore, in a very simple way, all the facts formulated in the law of contraction, and makes it directly intelligible why '*the disappearance of anelectrotonus is a much weaker stimulus than the appearance of katelectrotonus*,' since the polarisation-current is always weaker than the polarising, and both stimulate the nerve in a like manner, namely, at their negative pole.

If we bear in mind that the break-contraction arises through the passage of a current (the polarisation-current), we can quite simply formulate the law of contraction. We require in fact only two strengths of current:—

1. Weak currents, in which the excitation at the negative pole overpowers the blocking at the positive, and

2. Strong currents, in which the excitation at the negative pole is overpowered by the blocking at the positive.

These two cases comprise the whole law of contraction, if we only remember at the same time that every polarising current produces polarisation, and also, that every current, to liberate an excitation, must be of a certain strength.

During the closure of a current the excitability of the nerve is lowered in the region of the positive pole, both on the extrapolar and on the intrapolar side, and it is raised in the region of the negative pole.

Immediately after breaking, that is while the polarisation-current is still of sufficient strength, the excitability is seen to be diminished at the negative pole (the positive pole of the polarisation-current) and strengthened at the positive pole (the negative pole of the polarisation-current). Like the polarisation-current itself, the changes in excitability on breaking the polarising current are very evanescent. The agreement of the facts with the theory could not be more striking than it is.

After the stage of diminished excitability at the positive pole of the polarisation-current has passed off, a rise of excitability shows itself for a certain time throughout the whole extent of the nerve; and this phenomenon must be regarded as the real and only after-effect of the electric current.

Moreover, the circumstance that, in experiments on living animals and on nerves unseparated from their connections, only make-con-

tractions occur, is easily explained by my theory. Since the current can with the greatest ease branch off into all possible paths, its density in the nerve is so small that the polarisation cannot attain sufficient strength to liberate a contraction. This is possible only if very strong currents are used (Brenner [1]).

The experiments of Claude Bernard, Schiff, and Valentin, which are often cited in proof of the absence of a break-contraction on stimulation of living nerves, will not bear close examination. It is impossible to obtain exact results if, like Valentin, we insert electrodes directly into the thigh of an animal without dissection; the branch of the current which reaches the nerve with such a proceeding must always be very small [2]. The strength of the current employed by Claude Bernard, or rather by Rousseau, who performed the experiments in question, is nowhere given [3]. Chauveau confirms Claude Bernard's results, but adds that, when stronger currents are used, the break-contraction makes its appearance.

As to the strength of his currents Chauveau also says nothing; he merely assures us that the break-contraction appears with currents which do not alter the normal properties of nerve [4]; how the absence of the break-contraction in uninjured nerves can be deduced from this, I cannot conceive. Schiff too says nothing as to the arrangement of his experiments and the strengths of current which he used.

His assertions, therefore, cannot stand as evidence for the absence of break-contractions with uninjured nerves, the more so as he says himself that his law in general holds 'if the duration of the current is not too prolonged;' he subsequently admits that 'with considerably increased strengths of current' the second or third degree of contraction may be 'evoked with living nerves [5].'

'Living nerves,' according to Schiff, are therefore not quite insensible to the break-stimulus. The contrast between '*living*' and

[1] Hermann, Handbuch der Physiologie, i. p. 63, 1879.

[2] Valentin, Die Zuckungsgesetze des lebenden Nerven und Muskels, Leipzig und Heidelberg, 1863.

[3] Claude Bernard, Leçons sur la Physiologie et la Pathologie du Système nerveux, i. Paris, 1858, p. 185.

[4] Chauveau, Journal de la Physiologie, No. x, April, 1860, p. 283. 'It is certain that the passage of currents through motor nerves in the normal condition provokes contractions only at the moment of closing, whether the currents are ascending or descending. But it must be understood that we are using batteries sufficiently weak; otherwise the double contraction manifests itself even with the currents which are far from being sufficiently strong to alter the properties of the nerve and when the physiological conditions leave nothing to be desired.'

[5] Schiff, Lehrbuch der Physiologie des Menschen, i. pp. 80, 81, 1858–9.

injured nerves maintained by the enquirers named with reference to the break-contraction cannot therefore be regarded as established by faultless experiments.

In the numerous experiments relative to the law of contraction which I have made on nerves still connected with the spinal cord, I have never observed the break-contraction absent when its presence was to be expected, and when the experiment was rightly made.

My theory is as little capable of explaining opening tetanus as the laws of du Bois-Reymond and Pflüger are able to account for closing tetanus without a further assumption. The two phenomena are attributable to the same cause. The most likely theory, in my opinion, is that of Engelmann [1], according to which both closing and opening tetanus are dependent on a latent state of stimulation of the nerve from the influence of temperature, evaporation, or other causes. Of course this stimulation by itself is not sufficient to elicit tetanus, but it becomes so in parts of the nerve in which the excitability is increased; that is, in the neighbourhood of the negative pole after closure, and in that of the positive pole (the negative pole of the polarisation-current) after opening. This explanation may or may not be sufficiently complete; the chief point, in any case, is, that the opening tetanus is to be regarded as the equivalent of the closing tetanus; and I shall content myself in this paper with establishing a parallel between the phenomena occurring when a current is opened and those which present themselves when it is closed. In the breaking tetanus the excitation starts from the negative pole of the polarisation-current, which is what my theory requires.

The phenomenon of the 'voltaic alternatives' can be very simply explained by my theory. We know that, if a weak current is passed in the same direction with another current already traversing the nerve, its action is very considerably increased, since the exciting point now falls on a part of the nerve of which the excitability is increased. On the other hand, the excitation-effect by the closure of a weak current in the opposite direction is diminished, since the exciting point then falls on a part of the nerve where the excitability is lowered [2]. We shall see how the voltaic alternatives may be explained from this point of view.

We will suppose that the polarising current is ascending, because

[1] Engelmann, Archiv für die ges. Physiologie, iii. p. 411, 1870.

[2] Compare Grützner, Archiv für die ges. Physiologie, vol. 28, p. 143, 1882.

this direction favours the occurrence of a break-contraction, which again finds its explanation in this, that the polarisation-current is descending, and the excitation therefore encounters no obstacle in its progress to the muscle. If, now, the circumstances indicated by Engelmann are in operation, a tetanus occurs in place of a simple muscular contraction, when the current is broken. Supposing the polarising current is again passed in the same direction before the tetanus has ceased, the polarisation-current is arrested by the polarising current; the tetanus vanishes while the current is now passing the second time, it generates a new polarisation-current, which on interruption again produces tetanus. If now the direction of the current is reversed, and the current again closed, there is added to the polarisation-current another flowing in the same direction, so that their negative poles coincide; the tetanus must increase. The voltaic alternatives are thus necessary consequences of my theory.

I have thus proved the agreement between all the most important phenomena occurring when a polarising current is opened and the corresponding phenomena arising when it is closed. In order to subject the theory to a final test it still remains to examine whether it is in accordance with the recent researches of Biedermann and Grützner.

In a very thorough investigation Grützner[1] has shown the great importance of the nerve-current proper in relation to the result of electrical stimulation of nerves. All the phenomena with which Budge, Pflüger, Fleischl, and Hermann have made us acquainted relative to the excitability of different parts of a nerve, he explains by the action of the nerve-current, having proved that the current of an ordinary nerve-preparation takes a different direction at different spots, and that therefore the exciting action of a current is either strengthened or weakened, according as its direction is opposed to or coincides with that of the nerve-current.

In connection with these investigations Grützner also succeeded in showing the very great importance of the nerve-current as determining the opening contraction under certain circumstances. Let us suppose that by means of an ascending current we stimulate a divided nerve near its cut surface. The stimulating current is now flowing in the opposite direction to the nerve-current, and three things are possible; the stimulation-current may be weaker than the nerve-current, of the same strength, or stronger. If it is weaker

[1] Grützner, *loc. cit.* pp. 130–178.

than the nerve-current, or of the same strength, there will be no make-contraction, but this will appear whenever the stimulation-current is the stronger of the two. If the exciting current is weaker than the nerve-current the result is the same as if a weak ascending current flowed through the nerve during the whole period of closure; at the moment the exciting current is opened the nerve-current suddenly attains its full strength. Its negative pole now coincides with a part of the nerve which is in a state of heightened excitability due to the previous descending current. Through this rise of excitability the break-excitation becomes sufficiently strong to evoke a muscular contraction. If the stimulating current is of the same strength as the nerve-current, the latter is neutralized; when the stimulating current is broken the nerve-current appears in its full strength. Now, however, there is no part of the nerve endowed with a heightened excitability, and the break-stimulus by itself is too weak to generate a contraction. If the polarising current is still further strengthened, it overpowers the nerve-current and produces a polarisation, which, in conjunction with the nerve-current flowing in the same direction, calls forth a break-contraction.

Grützner's idea that the break-contraction which appears first is due to the nerve-current seems completely proved by the phenomenon of the 'gap' (Lücke) which he observed in his series of break-contractions. That the break-contractions occurring after the 'gap,' as to the origin of which Grützner has not expressed an opinion, do not owe their appearance to the nerve-current, is evident without discussion if we only bear in mind the actual conditions. But it is very easy to see why, after the gap, the break-contractions become stronger and stronger, for they are due to the polarisation-current, the strength of which increases with that of the exciting current.

Let us now suppose that a descending current is led through a divided nerve in the neighbourhood of the cut surface. This current must evoke a contraction even when of very weak strength, since it is added to the nerve-current flowing in the same direction. (For proofs of this see Grützner's papers above quoted, pp. 163, 167.) If the strength of the stimulating current is gradually increased, the contractions increase correspondingly to a maximum, and, as might be anticipated, no gap presents itself. When the current is broken, the polarisation-current flows in a direction opposed to that of the nerve-current. We can in this case, therefore, obtain a break-contraction only when the polarisation-current has become stronger

than the nerve-current. That this is actually the case may be seen from Grützner's experiments, p. 163.

Grützner further found that in the lower part of the sciatic nerve of the frog an ascending nerve-current exists. When therefore this part of the nerve is stimulated, the ascending break-contraction must show itself later than the descending, since in the latter case the nerve-current is added to the polarisation-current, while, in the first case, the two currents flow in opposite directions. At this result Grützner arrived experimentally. He stimulated the lowest part of the nerve and found a descending break-contraction when the rheochord slider stood at distances of 60, 45, and 690 mm, while he obtained an ascending break-contraction in the first case with a distance of 360mm, and in the two other instances failed to find it when the slider stood at 1000 mm (see *l. c.* p. 164). Just as, when the nerve was excited in the neighbourhood of the cut end, where of course the nerve-current is descending, so he found that on exciting the nerve in the neighbourhood of the muscle, where the nerve-current is ascending, there was a gap in the series of opening contractions (see p. 173).

Where the nerve is free from any current, i. e. at its middle, no difference is to be expected in the strength of current necessary for the appearance of make- and break-contractions respectively,—whatever may be the direction of the stimulating current. That this is actually the case is proved by Grützner's experiments (p. 164, 165).

The results found by Grützner are therefore not at variance with my theory of the break-contraction, but rather furnish new proofs of its correctness. Moreover, they afford indications of a new cause of the break-contraction under certain conditions, which has hitherto received from enquirers only a cursory attention. In proving more thoroughly than has before been done that the nerve-current is sometimes of sufficient strength to liberate a contraction, his results have supplied an additional support to my theory, since they have once more shown of how little consequence for the appearance of a contraction is the absolute strength of the current in comparison with several other circumstances, such as the abruptness of the increase of current strength, the condition of excitability, and so on.

I have already mentioned that some facts discovered by Biedermann agree very closely with my theory. His paper gives, besides, a number of new results which are in great measure explained by

Grützner's conclusions. Here we have only to enquire how far Biedermann's researches on the break-tetanus, with its associated phenomena, favour the theory that the break-contraction is determined by polarisation.

One of Biedermann's most remarkable results is the retardation of the break-contraction, which he obtained on treating the nerve with an alcoholic solution of common salt and with salts of potassium, and which he regarded as standing in the closest relationship to the break-tetanus. The reasons which he has adduced for this opinion appear absolutely conclusive, and furnish a new argument for Engelmann's well-known explanation. There is no direct connection between this retarded break-contraction and the ordinary one, as Biedermann himself states. The chief point is that, in this case also, the excitation proceeds from the positive pole (the negative pole of the polarisation-current), and that the susceptibility of the nerve to polarisation increases after treatment with alcohol.

Hitherto I have dealt exclusively with the contraction appearing when the current is completely opened. There is, however, another phenomenon described as a break-contraction, which shows itself when the polarising current is very suddenly weakened without being annulled. This contraction I have not studied at all, and the investigations made on the subject up to this time are too scanty to permit of a theory being formed with regard to it. We do not know with any certainty whence the excitation-effect comes, whether from the positive or from the negative pole. As Grützner in his paper (p. 143) states that he is engaged on the subject, I have not thought it well to commence any investigations upon it.

If, therefore, we leave out of account the case of the break-contraction evoked by a sudden weakening of the current, all the well-established facts, as I have endeavoured to show, point to the conclusion that *the break-contraction and all the phenomena occurring on breaking a polarising current are attributable to the polarisation-current, with which, in certain exceptional instances, the nerve-current co-operates.*

III.

ON THE

INTERNAL POLARISATION OF NERVES.

By Dr. ROBERT TIGERSTEDT.

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III.

After Peltier had demonstrated polarisation in muscle[1], du Bois-Reymond in the year 1856 showed that internal polarisability is encountered as a widespread property of animal tissues, including nerve and muscle[2]. Later (1867) he proved that this polarisability is incomparably stronger in nerve and muscle than in other bodies moistened with electrolytes, as well as that the strength of the polarisation increases with the duration of the current, up to a limit. This polarisation might arise in two ways. It might be external, at the junction of the muscle with the clay of the electrodes; and it might be in the substance of the muscle itself. He thought it unlikely that the first cause was here capable of an appreciable action. On the other hand, he demonstrated internal polarisability by so placing the electrodes of a galvanometer between those of the polarising current that the galvanometer was not acted on by the muscle while the polarising circuit was closed. After the polarising current had flowed through the muscle a sufficient length of time, with the galvanometer circuit open, the polarising circuit was opened and that of the galvanometer closed by a switch. A deflection ensued in the reverse direction to that corresponding to the polarising current in the muscle. Du Bois-Reymond obtained similar experimental results with nerves[3].

[1] Du Bois-Reymond, Untersuchungen über thierische Elektricität, i. 1848, p. 376 foll.

[2] Ibid. Gesammelte Abhandlungen, i. p. 19.

[3] Ibid. ii. pp. 191–193.

Meanwhile Matteucci had made similar observations. In several papers communicated to the Académie des Sciences of Paris from 1860 to 1867, he gave an account of his investigations on this subject[1]. His experimental method was faulty, and could by no possibility give exact results. He thus describes it, 'Lorsque le passage du courant a duré un certain temps, depuis quelques secondes jusqu'à 25–30 minutes, on enlève le nerf avec un support formé d'une lame de gutta-percha, et on le porte en contact des coussinets du galvanomètre, dont l'homogénéité a été reconnue d'avance'[2]. Besides demonstrating polarisation, and showing that it increases with the strength and duration of the current according to a law which he did not investigate more closely, he claims to have found that the electromotive force of polarisation is much stronger in the neighbourhood of the positive than in that of the negative pole. In proof of this he gives the following experiment. He passed the current (8–10 Daniells) an indefinite time (25–30 minutes and upwards) through a preparation consisting of two nerves. Afterwards the nerves were cut off and successively brought into the galvanometer circuit, arranged, however, in opposite directions. There then showed itself as difference of polarisation in the two nerves a current indicating that polarisation at the positive pole was stronger than elsewhere[3]. That an experiment so arranged proves nothing is evident without discussion. In contradiction to Matteucci's conclusions, du Bois-Reymond had found that, if the electrodes of the galvanometer are pushed along the conductor (that is the nerve) under investigation, without altering their distance from each other, equal deflections are obtained at all parts of the conductor[4].

In connection with his researches on electrotonus, Hermann made new investigations on the internal polarisation of nerves. To the results obtained by du Bois-Reymond he added observations on the duration and course of polarisation, which showed

[1] Matteucci, Comptes Rendus de l'Académie des Sciences, tom. 52, pp. 231–235, 1861; tom. 56, pp. 760–764, 1863; tom. 65, pp. 151–156, 1867.

[2] Ibid. tom. 52, p. 232, 1861. 'When the passage of the current has lasted for a certain time, from a few seconds up to 25–30 minutes, the nerve is removed on a support consisting of a plate of gutta-percha, and placed in contact with the electrodes of the galvanometer, it having been previously ascertained that they are homogeneous.'

[3] Ibid. tom. 65, p. 154, 1867.

[4] Du Bois-Reymond, Gesammelte Abhandlungen, i. p. 15. (The original is of the year 1856.)

that it continues for several minutes with constantly diminishing strength, and almost never entirely disappears, so that for a new experiment with the same tract of nerve, compensation must usually be employed to bring the needle to zero[1]. Hermann's conclusions relative to the electrotonic after-effect occurring outside the electrodes we need not consider in the following investigation.

Since then, no enquirer, so far as I know, has given a thorough study to the subject of internal polarisation in nerves. Yet a property which is so markedly conspicuous in nerve and muscle, as compared with other moist conductors, would seem to deserve investigation. Perhaps one might arrive at new and important points of view with regard to the way in which these tissues react to the electric current.

The investigations here communicated concern only nerves, partly because these appear to offer greater preliminary interest, partly because in muscle the contraction and the change of position which it entails exert a disturbing action on the investigation. In all probability the same laws hold good for the internal polarisation of muscle as for that of nerve. A future investigation will throw further light on this question.

In my experiments the polarising current was conducted to the nerves by the same electrodes as were used to lead the polarisation-current to the galvanometer. By this proceeding I hoped to be able to apply directly the results obtained to the phenomena which occur in excitation experiments with a constant current.

The experiments were arranged as follows. From the battery B_1 (fig. 3), the polarising current passes through a rheochord *Rh.* introduced as a derivation-circuit, to a Pohl's reverser R_1, and from there through a mercury key *K* and a Morse key *T* to the nerve *NN*, from which it returns to the reverser, and so on. Through the opposite arm of the Morse the current is taken to the galvanometer *G*. The 'rest-current' of the nerve is compensated in the usual manner by means of a du Bois' compensator *CC* (represented in the diagram as a straight line).

A spring *s* keeps one arm t_1 of the Morse pressed against the plate *a*, so that the contact t_2–b leading to the galvanometer is open. If contact is made at this point by pressing on the other

[1] Hermann, Untersuchungen zur Physiologie der Muskeln und Nerven, iii. pp. 71–74; Berlin, 1868.

arm t_2 of the Morse, the contact t_1–a is broken. The two contacts are carefully insulated by a plate of ebonite $1{\cdot}4^{mm}$ thick. The base-plate of the Morse key is cut in two, and a is isolated from b by a layer of pitch. In the diagram the continuous lines and arrows indicate the path and direction of the polarising current;

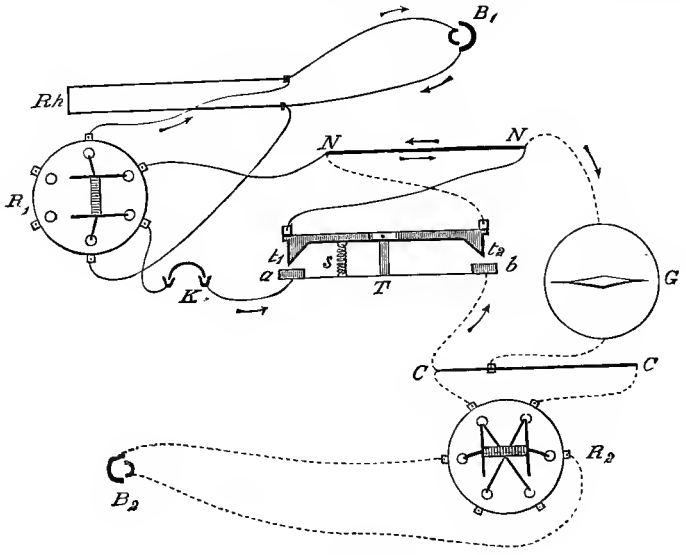

Fig. 3.

the dotted lines and arrows show the path and direction of the current going to the galvanometer.

There is therefore no possibility of the polarising current breaking into the circuit of the galvanometer. Du Bois-Reymond found, however, that such an insulation is not sufficient when strong currents are employed, inasmuch as, in spite of it, especially if the atmosphere is moist, there may be a slight escape of the polarising current to the galvanometer[1]. This drawback, however, did not interfere with the investigation. In the first place I used only pretty weak currents; the strongest being produced by 3 Meidinger's elements with 20,000 units in the rheochord. In the second place I was favoured in my work by dry weather, in consequence of which, for a long time, no action on the galvanometer from this source of error could be perceived. Even when the atmosphere became more highly charged with moisture and in consequence my gal-

[1] Du Bois-Reymond, Untersuchungen über thierische Elektricität, ii. Th. 1 Abth. p. 496, 1848.

vanometer was acted on when the circuit was open, the deflection even with 3 Meidingers and 20,000 rheochord units, did not exceed ·2 or at most ·3 divisions of the scale. With 3 Meidingers and 10,000 units it was from ·1 to ·2 div.; with 4000 rheochord units only ·1 div.; with 2000 no effect could be perceived. The errors which could possibly arise from this source lie therefore almost entirely within the common limits of errors of observation, as an examination of the experimental results shows.

As electrodes I used in most instances the large unpolarisable ones of du Bois-Reymond.

The polarising current was determined by means of a 'damped' and a periodic galvanometer. The distance of the telescope from the mirror of the instrument was 4400 mm.

To obtain a greater strength of current I used for every experiment the two sciatic nerves of a frog (*rana temporaria*) placed side by side. In all the experiments a battery of 3 Meidinger's elements was employed.

The experiments were conducted in the following way:—

The nerves are prepared and laid on the electrodes, while the key K is raised and the current thus shut off from the nerve. The 'nerve current' is compensated as exactly as possible. This done, and the Morse being depressed at b, the key K is closed. At a given moment the Morse is let go, and the spring now presses the arm t_1 against a so as to close the polarising current. After the polarising current has acted on the nerve for a given time, the arm t_2 is pressed against b so as to break the polarising current, and the polarisation current passes through the galvanometer.

To determine the time during which the polarising current flowed through the nerve I employed a metronome beating half seconds. After a few experiments I had got sufficient practice to carry out the necessary manipulations with the Morse; the following experiments may be cited as examples.

Experiment I.—3 Meidingers, 1000 rheochord units; duration of closure of current 5″; distance between the electrodes 11 mm.

No.	*Deflection.*
1	2·0
2	2·4
3	2·4
4	2·4
5	2·4
Mean	2·32

Mean variation ·13.

Experiment II.—3 Meidingers, 1000 rheochord units; duration of closure 5″; distance between the electrodes 11 mm.

No.	*Deviation.*
1	2·7
2	2·95
3	2·8
4	2·6
5	2·75
Mean	2·76

Mean variation ·092.

Experiment III.—3 Meidingers, 1000 rheochord units; duration of closure 5″; distance between the electrodes 10 mm.

No.	*Deviation.*
1	3·95
2	3·9
3	3·6
4	3·9
5	3·95
Mean	3·86

Mean variation ·104.

The time which elapsed between the opening of the polarising current and closing of the galvanometer circuit I tried to determine by means of a Depretz' signal. The following table contains the times thus arrived at:—

No.	*Time in Seconds.*	*No.*	*Time in Seconds.*	*No.*	*Time in Seconds.*
1	·029	12	·032	23	·027
2	·019	13	·033	24	·023
3	·018	14	·040	25	·021
4	·025	15	·031	26	·021
5	·024	16	·041	27	·021
6	·027	17	·032	28	·021
7	·032	18	·037	29	·022
8	·032	19	·037	30	·023
9	·032	20	·032	31	·023
10	·025	21	·030	32	·023
11	·025	22	·036	33	·023

The mean of these observations is ·028 seconds; the mean variation amounts to ·005 seconds.

In the Depretz signal, according to Marey[1], magnetization requires a period of $\frac{1}{200}''$, demagnetization $\frac{1}{500}''$. As a little consideration will show, the first of these numbers must be subtracted from, and the second added to, 0·028. We may regard these times as counterbalancing each other, and, this being the case, we have found that the time which elapses between the opening of the polarising circuit and the closing of the galvanometer circuit amounts to ·028 seconds with a mean variation of ·005 seconds. The extremes are ·018″ and ·041″. In general, therefore, we may say that the time in question ranges at highest between ·02″ and ·04″, a variation which for my purpose must be looked upon as quite immaterial.

My investigation of the laws of internal polarisation in nerves dealt mainly with the three following principal questions:—

(1) The dependence of polarisation on the strength of the polarising current.

(2) The dependence of polarisation on the time of closure of the polarising current.

(3) The durational course of polarisation.

In the descriptions of experiments *Rh.* denotes the number of rheochord units; *E*, the distance between the electrodes; *T*, the duration of closure of the current; *Sc*, the deflection of the galvanometer in divisions of the scale.

1. The dependence of polarisation on the strength of the polarising current.

In each of the experiments relating to this subject I led the current through the nerve for the same length of time, raising it gradually from a minimum (3 Meidinger, *Rh.* = 100) up to a maximum (3 Meidinger, *Rh.* = 20,000), which I did so gradually that no sudden alteration in the strength of polarisation could occur. The strengths of current which I used were expressed in terms of the number of rheochord units in the derivation-circuit, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 4500, 5000, 6000, 7000, 8000, 9000, 10000, 12000, 14000,

[1] Marey, La méthode graphique dans les sciences expérimentales, p. 476; Paris, 1878.

16000, 18000, 20000. The mutual relations between these strengths of current I determined by the deflection of the galvanometer, when the principal current went to the nerve and a branch of it was led off to the galvanometer by means of a Siemens' rheostat. In order to exclude, as far as possible, the effect of polarisation of the nerve, I passed the current through the nerve in both directions at each determination, and took the mean of the deflections obtained. The results are recorded in the following table:—

No.	*Rheochord units in the derivation circuit.*	*Sc.*	*Current strength Rh.* 100 = 1.
1	100	1·65	1
2	200	2·65	1·6
3	300	3·65	2·2
4	400	4·65	2·8
5	500	5·4	3·3
6	600	6·25	3·8
7	700	6·9	4·2
8	800	7·65	4·6
9	900	8·25	5
10	1,000	8·85	5·4
11	1,500	11·35	6·9
12	2,000	13·3	8·1
13	2,500	15	9·1
14	3,000	16·3	9·9
15	3,500	17·35	10·5
16	4,000	18·2	11
17	4,500	19·05	11·5
18	5,000	19·7	11·9
19	6,000	20·85	12·6
20	7,000	21·75	13·2
21	8,000	22·35	13·5
22	9,000	22·7	13·8
23	10,000	23·15	14
24	12,000	24	14·5
25	14,000	24·85	15·1
26	16,000	25·65	15·5
27	18,000	26·3	15·9
28	20,000	26·6	16·1

These values, with the corresponding rheochord units, are used in the records of experiment which follow. The following table comprises the results of a series of experiments relating to the subject:—

TABLE I.

No.	*R.*	*Current Strengths.*	*Numbers of experiments and readings of galvanometer.*						
			1	2	3	4	5	6	7
1	100	1	·5	·5	·45	·3	·45	·5	·3
2	200	1·6	·7	·75	·8	·75	·8	·8	·9
3	300	2·2	·9	·8	·9	·8	1·1	1·25	...
4	400	2·8	1	1·15	1·2	1·05	1·5	1·6	1·6
5	500	3·3	1·25	1·45	1·55	1·3	1·75	1·95	...
6	600	3·8	1·45	1·62	1·7	1·4	1·9	2·15	...
7	700	4·2	1·6	1·9	1·85	1·6	2·1	2·4	...
8	800	4·6	1·85	2·1	2·15	1·9	2·45	2·65	2·9
9	900	5	1·9	2·15	2·3	1·95	2·55	2·9	...
10	1,000	5·4	2·1	2·2	2·45	2·1	2·75	3·2	3·5
11	1,500	6·9	2·85	3·1	3·2	3·1	3·7	4·2	...
12	2,000	8·1	3·25	3·9	3·95	3·65	4·45	5·1	5·3
13	2,500	9·1	3·7	4·4	4·65	4·1	5·2	5·6	...
14	3,000	9·9	4·3	4·55	4·8	4·55	5·5	6·2	6·8
15	3,500	10·5	4·45	5	5·1	4·95	5·95	6·7	...
16	4,000	11	4·7	5·25	5·55	5·2	6·4	7·25	...
17	4,500	11·5	4·85	5·5	5·7	5·45	6·7	7·7	...
18	5,000	11·9	5·1	5·7	6·1	5·75	7	7·9	8·4
19	6,000	12·6	5·5	6·1	6·4	6·2	7·45	8·45	...
20	7,000	13·2	5·85	6·4	6·9	6·6	7·65	9	...
21	8,000	13·5	6	6·65	7	6·75	8	9·15	...
22	9,000	13·8	6·4	6·8	7·35	7	8·3	9·8	...
23	10,000	14	6·4	6·8	7·5	7·3	8·45	9·8	10·3
24	12,000	14·5	6·7	7·1	7·6	7·5	8·95	10·2	...
25	14,000	15·1	6·8	7·1	7·9	7·5	9·2	10·4	...
26	16,000	15·5	7	7·3	8	7·95	9·35	10·8	...
27	18,000	15·9	7·1	7·5	8·4	8·4	9·5	11·1	...
28	20,000	16·1	7·3	7·8	8·4	8·6	9·7	11·4	11·6

The distance between the electrodes was in

Experiment	1	...	...	30mm.
,,	2	...	...	35 ,,
,,	3	...	...	25 ,,
,,	4	...	...	30 ,,
,,	5	...	...	30 ,,
,,	6	...	...	25 ,,
,,	7	...	...	25 ,,

In all the experiments T was $= 5''$.

In order to make the irregularities of individual experiments compensate each other and to bring together the results of all the

experiments, I calculated the mean of the first six[1]. The numbers thus obtained are

No.	*Strength of the Current.*	*Sc.*
1	1	·45
2	1·6	·77
3	2·2	·96
4	2·8	1·25
5	3·3	1·54
6	3·8	1·7
7	4·2	1·9[1]
8	4·6	2·18
9	5	2·29
10	5·4	2·47
11	6·9	3·36
12	8·1	4·05
13	9·1	4·61
14	9·9	4·97
15	10·5	5·36
16	11	5·72
17	11·5	5·99
18	11·9	6·26
19	12·6	6·69
20	13·2	7·07
21	13·5	7·26
22	13·8	7·61
23	14	7·71
24	14·5	8·02
25	15·1	8·15
26	15·5	8·4
27	15·9	8·67
28	16·1	8·87

From these determinations it follows that *within the strengths of current employed in my experiments, the polarisation of the nerve is, as near as may be, directly proportional to the strength of the polarising current.*

2. The dependence of polarisation on the duration of closure of the polarising current.

To investigate this question I used a current of the same strength in all the experiments, and passed it through the nerve for unequal lengths of time, namely for periods of 1, 3, 5, 10, &c. seconds, and in some experiments of 240 seconds. At the end of each period the

[1] Experiment 7 I have not used in these calculations, as in it the individual determinations were too few.

galvanometer circuit was closed. A number of experimental records are exhibited in Table II.

TABLE II.

No.	*T.*	*Numbers of experiments and readings of galvanometer scale.*						
		8	9	10	11	12	13	14
1	1	1·3	1·2	1·45	1·2	1·6	1·5	1·5
2	3	1·9	2·05	2·2	2·1	3	2·7	2·6
3	5	2·15	2·55	2·4	2·5	3·5	3·5	3·3
4	10	2·5	2·9	2·65	3	4·35	4·6	4·3
5	20	2·95	3·6	3·2	3·7	5·2	5·7	5·05
6	30	3·15	3·9	3·5	4·15	6	6·1	6·15
7	45	3·45	4·05	3·7	4·5	6·6	6·5	6·6
8	60	3·65	4·65	3·85	4·75	6·6	6·9	7·
9	90	3·95	4·85	4·4	5·3	7	7·2	7·35
10	120	4·1	5·1	4·75	5·75	7·35	7·5	7·65
11	180	4·8	5·2	...	5·9	7·7	8·35	7·7
12	240	...	...	...	6·2	7·9	9	..

NOTE.—The distance between the electrodes and the strength of the current were in

Experiment	8	...	...		...	Rh. = 1000
,,	9	...	...	E. = 25mm.	...	,, = 1000
,,	10	...	...	E. = 15 ,,	...	,, = 1000
,,	11	...	...	E. = 30 ,,	...	,, = 1000
,,	12	...	...	E. = 30 ,,	...	,, = 2000
,,	13	...	...	E. = 20 ,,	...	,, = 1000
,,	14	...	...	E. = 23 ,,	...	,, = 1000

The means of the seven experiments (mean deflections for each duration of the closure) were as follows:—

No.	*T.*	*Sc.*
1	1	1·39
2	3	2·37
3	5	2·84
4	10	3·47
5	20	4·2
6	30	4·71
7	45	5·06
8	60	5·34
9	90	5·72
10	120	6·03
11	180	6·61[1]

[1] The values for a duration of the current amounting to 240″ are not counted in the mean, as they only enter into three experiments.

From all these experiments it appears: *that if the polarising current acts on the nerve for unequal and increasing lengths of time, other conditions being the same, the polarisation of the nerve increases, more rapidly at first, afterwards more and more slowly, finally approaching its maximum with extreme slowness.*

3. The duration and course of polarisation.

After the polarising current is opened, the polarisation remains at its height for only a short time, and then very rapidly declines. It lasts, however, as Hermann found, for a long time afterwards, though with very much diminished strength, so that it is always necessary to compensate the residual polarisation between every two experiments, as it would otherwise be impossible to bring an experiment to a conclusion.

To obtain a closer acquaintance with the duration and course of polarisation I proceeded as follows. I passed a current of definite strength through the nerve for a given time. Then I opened the polarising current at K (see diagram) and closed the galvanometer-circuit after intervals which differed in different observations. In this way I made myself acquainted with the residual polarisation. I performed the experiments in such a way, as, first of all, to close the galvanometer-circuit instantly after the polarising current was opened, just as in the experiments previously described. Then I closed the galvanometer-circuit 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 seconds and so on after the polarising-current was opened. In these experiments, then, the current passed along the nerve always for the same length of time, but the galvanometer-circuit was closed at different intervals after the current was broken.

These experiments are more difficult to carry out than the preceding ones with the simple appliances at my disposal, because the strength of polarisation falls off very rapidly, especially in the first seconds after interruption of the current, while, at the same time, the galvanometer-circuit has to be completed at the right moment with perfect accuracy. Still, the experiments recorded in Table III give an amply sufficient idea of the particular way in which polarisation falls off in nerves.

TABLE III.

No.	*Time after the current is opened.*	*Numbers of experiments and readings of galvanometer scale.*						
		15	16	17	18	19	20	21
1	0	5·15	6·55	7	7·8	7·15	7·4	11·7
2	1	3	3·8	4·1	4·25	4·4	5	9·5
3	2	2·3	3·1	2·6	2·2	2·3	4·3	7·5
4	3	1·8	2·4	2·35	1·75	1·65	2·3	4·4
5	4	1·7	1·9	2	1·25	1·4	1·8	3·5
6	5	1·55	1·5	1·8	·7	1·15	1·5	3·05
7	6	1·15	1·5	1·5	·65	1	1·15	2·65
8	7	·75	1·3	1·35	·55	·75	...	...
9	8	·6	1·05	...	...	...	1·05	1·7
10	9	·6	1·0	...	...	...	...	...
11	10	·6	·9	1·1	...	...	0·9	1·6
12	12	...	...	...	...	...	...	1·5
13	15	...	...	...	...	...	...	1·05
14	20	...	...	...	...	...	...	0·7
15	30	...	...	...	...	...	...	0·6

NOTE.—In all the experiments the polarising current was closed for 10 seconds. The distance between the electrodes, and the strength of the current used were in

Experiment	15	...	...	E. = 30$^{mm.}$	...	Rh. = 2000
,,	16	...	...	E. = 30 ,,	...	,, = 4000
,,	17	...	...	E. = 25 ,,	...	,, = 3000
,,	18	...	...	E. = 25 ,,	...	,, = 4000
,,	19	...	...	E. = 20 ,,	...	,, = 4000
,,	20	...	...	E. = 30 ,,	...	,, = 2000
,,	21	...	...	E. = 30 ,,	...	,, = 3000

The means of the deflections observed in experiments 15–20 for each duration of the interval between the opening of the polarising current and the closing of the galvanometer-circuit were as follows:

No.	*Time after opening of the polarising current.*	*Sc.*
1	0	6.84
2	1	4·09
3	2	2·80
4	3	2·04
5	4	1·68
6	5	1·37
7	6	1·16
8	10	0·88

From all these experiments it appears that *when the polarising current is opened, polarisation reaches its highest value instantaneously, and after that declines continuously. This decline proceeds at first very rapidly, afterwards more and more slowly, so that the polarisation lasts a long time after the current is shut off, and approaches the zero point only asymptotically.*

IV.

THE NATURE OF THE ELECTRICAL BREAK-EXCITATION.

By Dr. P. GRÜTZNER.

Pflüger's Archiv, Vol. xxxii. p. 357.

IV.

INTRODUCTION.

In a research carried on in conjunction with P. Moschner, student of medicine[1], I found that, in a large number of cases, the excitatory effect of break of a current passing through a nerve or muscle was in reality due, not to the disappearance, but to the appearance of the current: that there is thus a series of apparent break-excitations which are in reality make-excitations. These cases occurred when nerve-currents were present in the piece of nerve experimented on. As is well known, nerve-currents are of considerable magnitude in the neighbourhood of the cross-section, and have a most important influence on the effects of excitation. If, for instance, the nerve-current and the exciting current were in the same direction—if, that is to say, I excited with so-called 'like' currents—exceedingly weak currents sufficed to produce very great effects. If, on the other hand, I excited with 'counter-currents,' it was necessary to use very strong currents to elicit any response at all. When there was any response, it was far smaller other things being equal, than in the first case.

Excitation with counter-currents led us to a peculiar phenomenon hitherto unknown—the 'hiatus' in the series of apparent break-contractions. If one electrode was at the cross-section and the other a few mm. (5 to 7) away from it, and the nerve was excited with an ascending current, whose strength was gradually raised from zero, the following phenomena were observed. The break-contractions first increased in size: as the current strength was

[1] Pflüger's Archiv, vol. xxviii. p. 130.

raised further, they diminished, and finally disappeared: with still further increase of current strength they reappeared, at first small, but sooner or later attaining to a constant magnitude.

I explained the phenomenon as follows. If currents were passed in a direction opposite to that of the nerve-current, evidently three cases were possible. The counter-current was either smaller than, equal to, or greater than the nerve-current, and therefore either weakened it, reduced it to zero, or reversed it. The effect of opening this counter-current was that the nerve-current suddenly regained its original strength, in the first case from a diminished positive strength, in the second case from zero, and in the third case from a negative strength. In the first case, there was an excitation of the nerve; in the second, that is when the rise of current strength was from zero or near zero, no excitation[1]—this was the period of the hiatus; in the third case, again an excitation.

All these excitations observed at break, whether before or after the hiatus, were, however, in reality make-excitations, the excitation being always due to the rise of the nerve-current, either from a definite positive strength, an increase of current, or from a negative strength, a reversal of current. All these excitations I shall call neuro-electric or nerve-current excitations. Since they occur at break, and a new current is added to a previously existent current of the same or of opposite direction, I shall also refer to them as 'additive' in the same, or in the opposite direction. The break-excitations before the hiatus are therefore additive in the same direction, those after the hiatus are additive in the opposite direction; all being of course neuro-electric, and in reality break-excitations.

I may mention that about the same time as I made the investigations referred to above, Biedermann[2] and Hering[3] came to similar conclusions, they also finding that the excitation at break of an exciting current is, under certain circumstances, simply a make-excitation of the nerve-current. Hering has thus the credit of having first appreciated, in the case of muscle, the exciting effect of the nerve-current.

In speaking of compensation of the nerve-current by counter-currents, I do not, as mentioned in my previous paper, p. 170, refer to compensation of the nerve-current in the ordinary sense: not, that is to say, to currents which, as first employed by du Bois-

[1] [These observations are more fully referred to at p. 71.]

[2] Wiener Sitzungsberichte, lxxxv. Part 3, p. 144.

[3] Ibid. p. 237.

Reymond in his investigations, reduce to zero the part of the nerve-current led off by the electrodes, so that no current is indicated by a galvanometer inserted in the nerve-circuit, through which the two opposed currents pass.

I always employed, on the contrary, far stronger exciting currents. If, for instance, the nerve-current was compensated in the ordinary way by a derivation-circuit of 5 cm., the first break-contractions began with a derivation-circuit of 10 to 20 cm.

In this respect my experiments differ from those of Hering, who employed far weaker currents and very excitable preparations. Hering says that it is necessary for the success of his experiments that the frog's limb employed should be excited even by closure and opening of the nerve-current. In my first series of experiments I never used such preparations, and in my second, referred to in a preliminary communication [1], I did not particularly study their behaviour, since Hering had already thoroughly done so.

To prevent misunderstanding, or rather to remove those which have already arisen [2], I must further explain that I do not suppose that by compensating the nerve-current in the ordinary way I can reduce the currents present in a nerve to zero. On the contrary, a nerve, whose current is compensated in the ordinary way, behaves, as Hermann has clearly explained [3], like a nerve without any external circuit. Opening of a circuit through which a current exactly compensating the nerve- or muscle-current passes cannot, as was found by Hering and Biedermann and emphasised by Hermann, elicit any excitation in the nerve or muscle, for no electric change whatever is thereby occasioned in its fibres.

But the conditions are, I think, quite different if the currents used are not of the strength of ordinary compensation-currents, but far stronger. In this case it is really possible, by means of so-called over-compensation, to make the nerve currentless, if not in its whole length, yet assuredly in a certain part. With the exceedingly complicated conditions under consideration, it will, I think, be best to consider the nerve trunk in four sections, which are affected as follows by the strong counter-current. In the first, perhaps smallest, section, the nerve-currents are unaltered, their lines of flow differing too much from those of the counter-current for any alteration to be produced. In a second section, however, the nerve-

[1] Breslauer ärztliche Zeitschrift, 1882, No. 23.
[2] Virchow's Jahresbericht über Physiologie, by Gad, 1882, p. 193.
[3] Pflüger's Archiv, xxx. p. 14.

current will be weakened by the counter current; in a third reduced to zero; and in a fourth reversed. To these assumptions no one, I anticipate, will make any objection. I shall assume nothing more; for they are amply sufficient to render the phenomena which I observed, and my explanation of them intelligible.

Two additional points seem worthy of separate consideration. It might perhaps be objected that, since so many currents of different directions and strengths and taking different paths are passing in the nerve, it is impossible to say anything definite at all as to their effects. It would be necessary to suppose that the effects of the incompletely, the completely, and the over-compensated currents would manifest themselves simultaneously. This would be the case if all the fibres in the sciatic nerve were motor fibres of the gastrocnemius in which we are studying the effects of excitation. The motor fibres however form, if the sensory and other fibres in the sciatic are taken into consideration, perhaps a twelfth of all the fibres, according to a rough calculation. It is only, therefore, what occurs in that twelfth and its immediate neighbourhood that is of importance to us. The current-changes occurring in the remaining eleven-twelfths have no significance for us, or practically none. When, therefore, in the one above-mentioned twelfth of a nerve trunk the diminished nerve-current mounts at break of the counter-current to its original height, we have the break-contractions before the hiatus; when the nerve-current is exactly compensated, the hiatus; when it is over-compensated, the contractions after the hiatus.

Hermann[1] says, in connection with the subject of compensation of nerve-currents: 'It might be thought possible to do away with the demarcation-current altogether by over-compensating. This is, however, entirely impossible, since the lines of flow of the counter-current in the nerve run quite differently from those of the demarcation-current. Internal compensation is thus inconceivable, and the less so the nearer the proper electro-motive surface. The enormously strong currents in the immediate neighbourhood of the latter will be little affected by external currents ever so strong although these produce a special polarisation in the nerve.' I have nothing to object to this, nor does it contradict what I have said; for, as already mentioned, it is not necessary to my explanation of the hiatus that the demarcation-current should be entirely abolished.

[1] Pflüger's Archiv, xxx. p. 15.

Indeed, I can communicate several experiments which I performed in the summer session of 1882, in conjunction with Fräulein L. Nemerowsky, and which appear to me to confirm Hermann's assertion that internal compensation is the less conceivable the nearer one gets to the proper electro-motive surface. As is set forth in Fräulein Nemerowsky's dissertation[1], we have investigated the strength of the nerve-current, that is to say its electro-motive force, according as the electrodes, of which the one was always at the cross-section, were more or less separated from one another. If the electrodes are placed as near as possible, the electro-motive force of the current led off into the galvanometer is very small. It increases with the distance between the electrodes, and finally reaches a maximum when the electrodes are 5 to 7 mm. apart. With a yet greater separation of the electrodes it diminishes again, evidently because currents of opposite direction (ascending) now begin to be included[2], which diminish the strength of the descending current. If now, with a separation of electrodes of 5 to 7 mm., by far the greatest amount of current is led off by the external circuit, it is intelligible that in these circumstances the nerve-current will be most affected by over-compensation, since the electrodes, so to speak, include most current, and the lines of flow of the two currents differ from one another least. We have found as a fact that, since with electrodes close together it is impossible to abolish or weaken the nerve-current even by means of strong counter-currents, no hiatus appears, but the contractions first appear with much stronger exciting currents. The hiatus, however, is most marked when the nerve-currents are most influenced by over-compensation, that is, with a separation of electrodes of 5 to 7 mm.

By these explanations I believe that I have satisfied those who took exception to my theory of the hiatus[3].

As already mentioned above, I had, in studying with Moschner the phenomenon of the hiatus, opened and closed only in the main circuit. If a compensator (du Bois-Reymond's straight compensator) is used for regulating the strength of the exciting current,

[1] Über das Phänomen der Lücke, by L. Nemerowsky. Inaugural dissertation, Berne, 1883.

[2] See my paper on the above subject, Pflüger's Archiv, xxviii. p. 140.

[3] See also Biedermann (Wiener Sitzungsberichte, lxxxv. Abth. 3. p. 160), who has arrived at similar results in the case of muscle as ours in that of nerve, and has drawn similar conclusions.

the current may be led in to the nerve by closing the exciting current in the main or battery circuit, that is to say by placing a mercury key between element and compensator. But it is also possible to close the nerve-circuit after the main circuit by employing a key placed between electrodes and compensator.

Du Bois-Reymond[1] experimented with regard to this point with polarisable electrodes, and found marked differences in the effects of stimulation according as he employed the one or the other method. 'When I opened and closed the main circuit,' he says, 'contraction resulted with a length[2] of even a few cm., while often the whole length of the derivation-circuit wire (of about 2 m. long) was insufficient to evoke contraction on opening and closing the nerve-circuit. Immediate excitation of muscle showed the same difference, but between limits whose absolute values were higher.'

Du Bois-Reymond's explanation is as follows: 'When the main circuit is closed after the nerve-circuit, the one division of the current enters the nerve-circuit with an intensity conditioned by the relationship of the resistances. When the main circuit is opened, the current which is abolished in the nerve-circuit has been previously reduced to a minimum by polarisation. But the latter current, since a path is left open through the derivation-circuit, is immediately followed by the polarisation-current in the opposite direction, whose strength is perhaps equal at first to that of the primary current, and which is therefore well suited to elicit contractions. The charges are for the most part got rid of instantaneously in the polarisation-current, so that, when the key in the main circuit is again closed, the same series of events is repeated. If, however, the nerve-circuit is closed after the main circuit, the current strength will be the same at the first closure as at closing the main circuit after the nerve-circuit. Since, however, opening the nerve-circuit prevents the charges which immediately develop from discharging themselves, opening of this circuit is comparatively inoperative, and, secondly, the current strength at closure after a not too long interval will not be so great as before.'

In the more or less complete leading off of the external polarisation-current arising between electrodes and nerve-tissue, du Bois-Reymond thus finds the explauation of this striking difference.

[1] Ges. Abhandlungen, i. p. 196, 1875.

[2] That is, the wire of the compensator or rheochord used. See diagram on a subsequent page.

When, however, unpolarisable electrodes are employed, there is no longer the same difference.

More recently Biedermann and Hering[1], the former with parallel-fibred curarised muscles, the latter with exceedingly excitable nerve-muscle preparations (both using unpolarisable electrodes), made similar experiments, and convinced themselves that excitation of a muscle or a nerve by its own current can, for instance, occur if a good external arc of connection is offered to these currents, that is on closure of an arc whose ends are at the cross-section and at the surface, or, what comes to the same thing, on breaking the counter-current in the battery circuit in the case of a nerve- or muscle-current compensated in the ordinary way. Similarly, contractions are observed if the arc of connection is broken, or, what comes to the same, if the compensating counter-current is closed in the battery-circuit. But there is no excitation if, with the nerve- or muscle-current compensated, the key in the nerve-circuit is opened, or if, with the nerve-circuit previously opened, a compensating counter-current is directed through the nerve by closure of the nerve-circuit.

When the current is stronger than necessary for compensation in the ordinary sense, the conditions become more complicated, but most readily intelligible if what was said at p. 95 on this subject is borne in mind. Hering gives the following explanation of the facts in this case, simultaneously observed by him and by me, namely, that excitation with counter-currents has more effect if the current is made and broken in the main circuit than if in the nerve-circuit, that is, that in the first case weaker currents are able to elicit contractions. 'When the counter-current is somewhat stronger than necessary for compensation, after closure of both circuits the current in the nerve is actually ascending, although only traversed by what may be called the remainder of the battery-current. Thus if, with the main circuit already closed, the nerve-circuit is closed, there is no contraction unless the division of the battery-current passing through the nerve-circuit is of very considerable strength. If, on the other hand, the main circuit is closed with the nerve-circuit already closed, the effect of opening the nerve-current is added to the weak and, by itself, insufficient effect of closure of the division of the battery-current, and a contraction occurs. On opening the nerve-circuit with the main circuit previously closed, no contraction occurs, always provided that the division of the battery-circuit

[1] Wiener Sitzungsberichte, lxxxv. Part 3. p. 144; ibid. p. 237.

ascending in the nerve is not so strong as to produce a break-excitation by itself, in spite of its partial compensation by the nerve-current. On opening the main circuit with the nerve-circuit closed, a new path is afforded to the nerve-current, and a contraction occurs, which is here further reinforced by the influence of the Voltaic alternatives. For, if the influence of the latter depends on the fact that a point on a nerve which had previously been the point of entrance of a current has become more sensitive to excitation by a current leaving the nerve at the same point, the effect of closing the nerve-current will be greater. I shall here entirely neglect any effects which polarisation-currents might have, since these currents would find a path for discharge by the nerve-circuit at break of the main circuit.'

While refraining from all further criticism of Hering's explanations, I yet think that they are at least insufficient. It appears to me that the circumstance which Hering puts aside altogether, the formation namely of polarisation-currents, is of far greater importance than the other facts. I believe that all these phenomena may be explained in the most simple manner as follows. If a battery of inconstant strength is closed through an arc of connection of small resistance, the electromotive force of the battery, as is well known, quickly falls off from the formation of a polarisation-current, and any one who has once used such a battery for galvano-caustic experiments knows how quickly the wire ceases to glow when the current has been passed for some time, and, on the other hand, how quickly and certainly it again becomes red-hot on closure after the battery has been left open for a short time; further, how little the electromotive force diminishes if there is a circuit of great resistance.

Now a nerve, or at any rate certain parts of it, when an arc of connection of small resistance is applied to it, is analogous to a battery whose current diminishes very rapidly; while a nerve without any such arc of connection is analogous to a battery closed by a circuit of very great resistance.

Hence if the current is broken in the battery circuit, thus leaving for the nerve an external arc of connection always closed, the counter-current has at closure only to contend with a weak current in the portion of nerve concerned, and will therefore produce an effect sooner; hence the earlier appearance of excitation on closing the counter-current in the main circuit. The opposite of course occurs on closure in the nerve-circuit. On opening in the battery

circuit the nerve-current which appears in the piece of nerve concerned passes more easily along the constantly closed external arc of connection than through the nerve substance; hence the earlier occurrence of what appear to be break-excitations on opening the battery circuit.

A similar explanation, it may be remarked, holds for the fact, also discovered by Hering and me, that with a 'like' exciting current excitation appears earlier when the current is closed and opened in the nerve-circuit. For in this case also we have a nerve with a stronger current in the parts concerned, since there is no opportunity for the current to discharge itself through an external arc of small resistance, and so fall off in strength from internal polarisation. Closure in the nerve-circuit of a like current thus causes alteration from a higher ordinate than closure in the main circuit. The former is therefore more operative, that is to say weaker exciting currents can excite the nerve, because they find it so to speak more strongly electrotonised, and therefore in a more excitable condition.

I have had little experience of the excitatory effects of like currents, as I observed scarcely any break-excitations at all with the current strengths used by me. I shall therefore refrain from discussing this subject. Hering's explanation is as follows: 'On closure in the main circuit the nerve-current previously passing into the electrode applied to the surface of the nerve is only reinforced by the arrival of the battery-current. But if the nerve-circuit is closed after the main circuit, the nerve- and battery-currents are closed at the same moment, and hence the effect of closure will be greater in the latter case. Similarly, the two currents disappear simultaneously on opening in the nerve-circuit.'

Although, as already said, this subject must be left undiscussed, I nevertheless believe with regard to the effects of closure that my experiments[1], which have lately been confirmed and extended by Hermann[2], show that the rise of a current from zero to a considerable height has far less excitatory effect than even a very slight rise beginning, not at zero, but at a definite positive height. Hence, if Hering's assumption were correct, closure in the nerve-circuit would be less operative than closure in the main circuit, which, however, is not the case.

It should be noted that all these phenomena appear constantly

[1] Pflüger's Archiv, xxviii. p. 144.
[2] Ibid. xxx. pp. 11 and 12.

only when the electrodes are at a moderate distance (5 to 7 mm.) apart. With the electrodes closer there is no difference observable, or there may even be a difference in the opposite direction. With the electrodes at indifferent points we have, as might be expected, never been able to observe a difference in the above sense. Contractions begin with exactly the same current strengths, whether the current is opened and closed in the main or in the nerve-circuit.

THE BREAK-EXCITATION.

It had thus been shown—and therefore I referred to these experiments again here—that (1) a large class of break-excitations are only so apparently, and (2) that the excitation of a particular set of fibres in a nerve-trunk may be due to the closure of a current in the substance of the nerve, independently of the existence of an external arc of connection. Since, further, I had by earlier experiments convinced myself that (3) in the case of currentless nerve or muscle preparations excitation either does not occur at all at break, or only with very strong currents, there naturally arose a doubt in my mind as to whether the disappearance of an electric current ever excites a nerve or muscle; whether, to speak with Pflüger, the disappearance of anelectrotonus does in reality produce an excitatory effect. I now think that this is not the case, and believe, moreover, that *there is no break-excitation,* but that every so-called break-excitation is in reality a make-excitation.

Before, however, I say anything as to my reasons for this belief, I wish to express my pleasure on finding that about the same time R. Tigerstedt[1] arrived at exactly the same conclusions, from similar experiments and reasoning. This fact points, I think, with a certain probability to our mutual view of the matter being the right one. As Tigerstedt's work is doubtless accessible and known to the readers of this paper, I can pass more rapidly over many points, and refer the reader to that work.

Apart from the mention of the matter by Peltier[2], du Bois-Reymond[3], as is well known, was the first to prove by unimpeachable experiments that in a nerve or muscle through which a current has been passed there is afterwards a current in the opposite direction.

[1] See No. III of these Translations, of which the original appeared two or three months after the author's preliminary paper (Breslauer ärztliche Zeitschrift, No. 23, 1882).

[2] Untersuchungen über thierische Elektricität, i. p. 376, 1848.

[3] Ibid. p. 377.

Although Peltier attributes to this secondary polarisation-current the excitatory effect on breaking the original, primary current, this hypothesis was discredited by the authority of du Bois-Reymond, and first became known to me on reading through the literature of the subject after I had reached, on the above-mentioned grounds, my conclusions as to the nature of the break-excitation. 'In what way Peltier meant to explain the break-contraction by means of this fact,' says du Bois-Reymond, 'it is not easy to understand, since these charges require to all appearances a closed circuit to produce a current through the nerve; this condition however is lost at break.'

Now this main objection is no longer valid; for I convinced myself that in the above-mentioned experiments breaking the nerve-circuit allowed the nerve-current to come into existence by being closed through certain paths in the nerve, and so caused excitation. Although, so far as I know, there are no other similar observations on the excitatory effect of a current whose circuit lies wholly in the nerve, yet it was generally assumed that nerve-currents partly close themselves within nerves[1]. It therefore seemed to me quite incomprehensible that no significance with regard to the break-excitation had been attributed to this secondary polarisation-current, and the more so that this polarisation-current had been recently investigated by various observers under the name of secondary electromotive phenomena[2]. I have lately turned my attention to this polarisation-current, since in it is to be found, as it seems to me, the real cause of the break-excitation. The results of my investigations may be summed up in few words.

Unpolarisable electrodes were applied to a nerve or muscle (curarised sartorius) at indifferent points 6–10 mm. apart, and so connected with a Pohl's reverser without cross-wires that in the one position of the reverser the polarising current, of from a given fraction of a Daniell up to three Daniells at the highest, flowed through the nerve, while in the other position the secondary current generated in the nerve flowed through a Wiedemann's galvanometer. Turning over the reverser occupied a fifth of a second on an average.

I observed, in full agreement with Tigerstedt, that (1) the secondary polarisation-current increases correspondingly to, and approximately in proportion to the strength of the polarising

[1] Cf. Hermann, Handbuch der Physiologie, ii. p. 180.
[2] Ibid. ii. p. 164.

current; that (2) the polarisation-current increases with the duration of the polarising current. My observations were however only continued over shorter periods than those of Tigerstedt. Nevertheless in them too the law became evident that the greatest effect is produced in the first seconds during which the polarising current remains closed and that a more prolonged closure of the primary current only increases the secondary current to a slight extent. (3) I investigated in exactly the same way as Tigerstedt the rate at which the polarisation-current disappears from the nerve, and found, although more time elapsed in my experiments than in those of Tigerstedt between the moment of opening the primary current and closing the galvanometer-circuit, that the secondary polarisation-current is stongest during the first moments after closure, and then gradually becomes weaker, first quickly, and afterwards slowly, but that it can still be observed for a very long time—in the case of muscle after the lapse of minutes.

Quite recently there was published a thorough investigation of this subject by du Bois-Reymond, in which a very important and altogether new fact was brought to light, namely that of *positive* polarisation. Du Bois-Reymond found that if a current is passed through a muscle or nerve, and its electrical condition immediately after opening tested by means of a second pair of electrodes placed between those of the polarising current and connected with a galvanometer, under certain conditions positive polarisation appears at first, that is to say there is a current with the direction of the primary current, while negative polarisation does not appear until later. Like Tigerstedt [1], I have not observed this positive polarisation in my experiments, doubtless for the simple reason that I used primary currents of insufficient strength, and further that my periods of break—the periods of time, that is to say, elapsing between the breaking of the primary current and making of the galvanometer-circuit—and of make were too long. For du Bois-Reymond observed strongest positive polarisation in muscle with a make of ·075 seconds' duration and a current of twenty Groves. If the duration of make in the case of nerve was longer than a second, polarisation was always negative; and the weaker the primary current, the earlier did negative polarisation appear. Now even if the polarisation indicated by the galvanometer is to be regarded as the algebraical sum of the two kinds of

[1] Sitzungsberichte der Akademie der Wissenschaften zu Berlin, Sitzung 5 April, 1883, p. 343.

polarisation, yet this resulting polarisation is alone of importance here, since we only used weak currents (usually of less than one Daniell) in our excitation-experiments, and closed the exciting current for a period of a second on an average. We therefore consider it safe to assume that in these experiments positive polarisation has never occurred, or, to put it otherwise, has always been more than compensated by far stronger negative polarisation.

However important, then, this positive polarisation may be in itself, we may treat it as if it had been absent in our experiments.

The further part of our task, namely to show that the cause of the break-excitation is to be sought, not in the disappearance of a current, but in the appearance of the (negative) polarisation-current, is now very easy. We shall bring together all the cases in which break-excitations have been observed, and endeavour to determine for each case whether there can be a polarisation-current in the nerve without external connection.

We shall first consider the law of contraction as it occurs when the unpolarisable electrodes have been applied to a nerve at indifferent points. In this case the effect, in so far as shown in the muscle, of closure of descending currents (which closure elicits a response with currents of a certain strength and upwards), increases with increase of the strength of current, but soon reaches a maximum at which it remains. Break-excitations with ascending currents follow exactly the same law, except that they require stronger currents for their first production.

On the other hand, it is known that make-contractions with ascending currents increase with the strength of current up to a certain current-strength, but decrease with greater current-strengths until at last they disappear altogether. Break-contractions with descending currents follow the same law, except that they also require stronger currents for their first production.

The fact that the phenomena group themselves into these two series is readibly intelligible on our hypothesis; for the opening of descending currents is equivalent to the closure of weaker ascending ones, while the opening of ascending currents is equivalent to the closure of descending ones.

Excitation of a muscle or nerve, as Pflüger, von Bezold, Engelmann, and Biedermann have shown, occurs at a pole—on closure at the cathode, and on opening at the anode. The latter excitation is also the weaker. We should say, however, that the excitatory

action of a current occurs only on closure and at the cathode; the excitatory effect of opening a current begins, no doubt, at its anode, but only because this is the cathode of the polarisation-current at closure.

In the region of the anode there is diminished excitability, and with strong currents excitations cannot be transmitted from the anode; hence the diminution and disappearance of the make-contraction with an ascending current, and, we now add, the diminution and disappearance of the break-contraction with a descending current; for just as in the previous case there was an obstruction at the anode to the transmission of an excitation to the muscle, so now there is an obstruction at the anode of the polarisation-current.

On opening a polarising current there is, as is well known, diminished excitability immediately afterwards in the region of the cathode, increased excitability in the region of the anode. The relation has apparently been reversed, but on our hypothesis remains just the same; for in the one case the cathode of the primary current, while in the other the anode of the primary current, is cathode to the polarisation-current.

The above, as the reader will admit, is a series of very remarkable agreements between what our hypothesis demands and the actual facts. This agreement, however, holds still further. The well-known 'Voltaic alternatives' consist in the fact that a nerve or muscle through which a current has been passed for some time becomes very sensitive to closure of a current of opposite direction, while its sensibility to a current of the same direction is diminished. The explanation is simple—that the second current is, in the one case in the same direction as the polarisation-current, in the other case in the opposite direction.

If our hypothesis as to the nature of the break-excitation is correct, the stronger the secondary polarisation-current, and the less the resistance it encounters, the earlier will a break-contraction occur, provided always that its anode does not block the way from the point of excitation to the muscle. Now my investigations and Tigerstedt's have proved that within the periods taken for stimulation-experiments the strength of the polarisation-current increases with the duration of closure of the polarising current. Nothing is easier to show than that with equal strengths of current break-contractions occur much more readily if the current is kept closed a little longer. Small fractions of a second make

great differences here, since usually the exciting current is kept closed for barely a second.

It is an analogous fact that if with a weak current there is no break-contraction, one occurs if a stronger current, at the opening of which there may have been an excitation, be first passed through the nerve in the same direction. For the nerve is strongly polarised by the last-mentioned current; the quickly following opening of a weak current, which previously had no effect, now elicits a contraction, since there is now a stronger polarisation-current than before. This is also the explanation of the fact that the phenomenon of the 'hiatus' discovered by me, did not appear, or at least not usually, when I changed the current from a higher to a lower strength. Biedermann[1] and Tigerstedt[2] recently observed similar facts.

The strength of the polarisation-current increases, moreover, with the strength of the primary current; hence it is that at indifferent points in a nerve or muscle break-contractions do not occur until strong exciting currents are employed, and increase with the current strength.

Tigerstedt has also found that the sciatic nerve of a frog is easier to polarise near the point of section, or after dilute alcohol has been applied to it. Both these conditions also favour the occurrence of break-contractions, as was shown by my earlier experiments, and those of Biedermann.

The polarisation-current can also be increased by the use of polarisable, instead of unpolarisable electrodes. In this case there is an external polarisation-current between the metal and moist nerve, and an internal one between the various constituents of the nerve. As, however, the closure through the nerve of the external polarisation-current is determined by the same, or nearly the same conditions as determine that of the internal one, and as the former current is added to the latter, a series of phenomena which depend on the closure through the nerve of polarisation-currents are in this case unusually well-marked. It is thus very easy to convince oneself that if instead of unpolarisable electrodes ordinary metallic electrodes are used, and with the same resistance, in order that the conditions may be as like as possible, break-contractions at break of the main-circuit always appear earlier than when unpolarisable electrodes are used. An experiment may be cited to exemplify this.

[1] Wiener Sitzungsberichte, Part iii. vol. lxxxiii. p. 328, 1881.

[2] Tigerstedt, p. 55 of this book.

EXPERIMENT.—A nerve-muscle preparation from a Rana esculenta of moderate size is arranged in a Pflüger's myograph. The electrodes are placed on the nerve at indifferent points, the proximal one at about 30 mm. from the cut end, which is held by a thread, the distal at about 12 mm. from the muscle and 7 mm. from the proximal one. The current is of one Daniell. Mercury keys are inserted in both the main and the nerve circuit. As derivation-circuit (rheochord) I used in these and other experiments three German-silver wires stretched backwards and forwards parallel to one another on a board, and each 1 metre long and ·5 mm. in cross-section. Contact of one of the electrodes, which was movable, with the wire was brought about by means of a pair of forceps, made on the principle of ordinary spring-forceps and well nickel-plated, which rode on the wire. The blades of the forceps were thick and heavy at their ends, so that they kept fast. At their other end the forceps carried a small screw, by which the electrode wire was fixed. As the derivation-circuit wire was carried well clear of the board, the forceps could be very easily applied at any desired point on a wire, or transferred from one wire to the other. I can recommend this as a very practical arrangement. It appears to me to be both neater and more certain than the mercury contact in du Bois-Reymond's rheochord.

The following experiments were made for comparison. Firstly, the break-contractions were compared with one another as to size when the current was opened only in the nerve-circuit, (*a*) with unpolarisable and (*b*) with polarisable electrodes; secondly, when the current was opened only in the main circuit. There are thus the following four cases:—

A. Current opened in the nerve-circuit ... { *a*. Unpolarisable electrodes (1) / *b*. Polarisable ,, (2)

B. Current opened in the main circuit ... { *a*. Unpolarisable electrodes (3) / *b*. Polarisable ,, (4)

We shall first compare cases 1 and 2, and 3 and 4. Afterwards (see below) cases 1 and 3, and 2 and 4 will also be compared.

The following is the record of the experiments:—

First Break-contraction.

Experiment 1:—

In case 1 no contraction up to 300 cm. derivation-circuit (rheochord wire).
,, 2 ,, ,, 300 ,, ,, ,,
,, 3 contraction began at 275 ,, ,, ,,
,, 4 ,, ,, 30 ,, ,, ,,

Experiment 2:—

In case 1 no contraction up to 300 cm. derivation-circuit.
,, 2 ,, ,, 300 ,, ,, ,,
,, 3 contraction began at 260 ,, ,, ,,
,, 4 ,, ,, 40 ,, ,, ,,

In experiment 1 the exciting current was ascending, in experiment 2 descending.

Two additional experiments, in which the conditions were exactly the same as in the two first ones, gave the following results:—

First Break-contraction.

Experiment 1:—

In case 1 contraction began at 285 cm. derivation-circuit.
,, 2 no contraction up to 300 ,, ,, ,,
,, 3 contraction began at 230 ,, ,, ,,
,, 4 ,, ,, 35 ,, ,, ,,

Experiment 2:—

In case 1 no contraction up to 300 cm. derivation-circuit.
,, 2 ,, ,, 300 ,, ,, ,,
,, 3 contraction began at 260 ,, ,, ,,
,, 4 ,, ,, 40 ,, ,, ,,

In a fourth experiment, for which a current of two Daniells was used, the first break-contractions occurred with the following values of the derivation-circuit, counting in the same order. With ascending current at 170, 220, 150, 50; with descending current at 190, 280, 160, 60. In order to have the resistance equal in cases 1 and 2, and in cases 3 and 4, when the metallic electrodes were placed on the nerve the previously used impolarisable electrodes were brought into the nerve- or muscle-circuit, lying end to end.

Thus when the external polarisation-current is added to the internal the occurrence of break-contractions on opening the main circuit is favoured, as is evident from the experiments and readily intelligible. (Compare cases 3 with cases 4.) If, however, the current is opened in the nerve-circuit, the rule is that the occurrence of break-contractions is not only not favoured, but even hindered. (See cases 1 and 2 in the second series, with ascending current.) This would seem to mean that there is far less resistance to an internal polarisation-circuit lying altogether in the nerve, than to a similar external one. To this point I have not further directed my attention.

Muscle behaves like nerve according as polarisable or unpolarisable electrodes are used and the main circuit is opened.

EXPERIMENT.—A sartorius muscle of a medium-sized curarised grass-frog is laid on the electrodes in such a way that no muscle-current passes through them (position of indifference). Two Daniells. There was a break-contraction for both ascending and descending currents in case 3 (polarisable electrodes, main current opened) with 190 cm. of wire. In all other cases no break-contraction up to 300 cm. of wire. With a current of six carbon-zinc elements a similar result. Break-contraction only in case 3 with 80 cm., in all other cases no break-contraction up to 300 cm. Arrangement similar to that of the previous experiments.

We now arrive at the consideration of those cases in which the secondary polarisation-current through the tissue to be excited is of insufficient density, or for any other reason fails.

A number of both earlier and more recent observers (Cl. Bernard, Schiff, Valentin, Fick, Rumpf) have drawn attention to the fact that break-contractions occur less readily with uninjured nerves in the living animal than with those which have been cut across and prepared. There are clearly two causes for this. On the one hand the continuance of the circulation must oppose polarisation by removing its products, on the other hand when a nerve is not insulated and lying on the electrodes the polarisation-current can pass along other paths, so that the current passing through the nerve is weakened.

There is a fact which is evidently related in nature, and is easy enough to observe, though, so far as I know, it has not been more

closely investigated by physiologists. Ritter, as is well known, first maintained that there is a special law of contraction for the thigh of the frog as a whole, and called attention to a difference with respect to excitation between the flexors and extensors.

The truth of this much-questioned assertion of difference in excitability between physiologically different groups of muscles was established by Rollet, and is confirmed by recent investigations of my own, which will shortly be published. This difference manifests itself at closure and opening in the fact that the more powerful stimulus affects the less excitable extensors most, while the weaker stimulus has most effect on the more excitable flexors. Thus, if one applies a pair of either polarisable or unpolarisable electrodes to the sciatic nerve of a frog at a point midway between its point of exit from the spinal cord and the point where it disappears in the thigh, care being taken that they are kept in exactly the same position, it will not be observed that as the strength of the currents employed is raised the same group of muscles merely contract more and more strongly, but that quite different muscles contract with weak and strong currents respectively[1]. If one carefully observes which muscles first contract at closure of weak currents (usually certain muscles of the thigh and toes), the interesting fact will be observed that on further increase of the current-strength other muscles are excited, and always more and more strongly at closure, while at opening those muscles alone contract which had previously contracted with weak currents at closure. The break-excitations of these relatively strong currents are now similar in their effect to make-excitations of the weak currents.

Similar phenomena occur in human muscles, and I am astonished to find no mention of them in handbooks of electro-therapeutics. For instance, if with a sufficiently strong current the electrodes are placed a few centimetres apart in the groove on the inside of the biceps, it will be observed constantly that with certain current-strengths other muscles contract at closure than at opening. I often noticed strong flexion of the hand on closure, and moderate pronation on opening the same current.

In experiments on man (which I have only made cursorily, and intend to pursue further when I have an opportunity) the conditions are of course not so apparent as in the case of separated frogs' nerves. It can be more particularly objected that if the electrodes are sufficiently far apart the points of excitation are also far apart, and

[1] See the dissertation of L. Nemerowsky, Berne, 1883.

hence that on closing and opening a current the same nerve is not acted on with different current-strengths, but different nerves are acted on at closure and opening, which, I believe, may often enough happen. For if the break-stimulation of a current is really nothing else than the make-stimulation of its polarisation-current, it is conceivable that in the above experiment on man the battery-current, which enters the body at one electrode and leaves it at the other, may flow along paths different from those of the polarisation-current, whose circuit must be completed through the tissues alone and which may therefore stimulate other nerves.

This experiment brings us to a new fact, which, though it is connected with experiments previously noticed (p. 108), must be separately considered here. As already mentioned, neuro-electric, additive break-contractions appear earlier at break of the main than of the nerve-circuit. The nerve-current which acts here as stimulus meets with less resistance in its passage along the derivation-circuit than in the substance of the nerve. What is true of the nerve-current is true also of the current of internal polarisation. It is therefore easy to show that if unpolarisable electrodes are applied to a nerve at indifferent points, i.e. where there is no nerve-current, break-contractions appear earlier if the current is broken in the main circuit than if in the nerve-circuit. This will be evident if cases 1 are compared with the corresponding cases 3 in the experiments at page 109. In each series, i. e., the length of wire required to elicit the first break-contraction is greater in case 1 than in case 3; thus 300 is greater than 275, and so on. In case 1 the current was made and broken in the nerve-circuit, in case 3 in the main circuit.

Hermann made similar experiments four years ago, but did not publish them until shortly after the publication of my preliminary communication and of Tigerstedt's complete paper. He also concludes from his experiments, the results of which, interesting to us, he thus summarises, that 'where the break-contraction is struggling for existence it appears if there is any difference at all with weaker currents and is stronger if the current is broken in the main circuit than if in the nerve-circuit.' Hence he concludes that the counter-current due to polarisation is concerned in the production of the break-contraction. In my opinion Hermann was not justified in drawing this conclusion from the above-mentioned experiments, for the reason that though his experiments were made a long time ago, he has only now drawn the conclusion from them, or at least

published it. Thus there are wanting in Hermann's investigations the exceedingly important control experiments to determine whether the excitation at break of the primary current is due entirely or principally to the polarisation-current. He might quite as well have been dealing with apparent, additive break-contractions due to the appearance of the nerve-current. To judge from my own experience, it is exceedingly probable that such might have been the case, since as a rule the electrodes are so applied to a nerve that nerve-currents pass through them. The earlier appearance of break-contractions with descending currents, which Hermann records, appears to me to point to additive break-contractions being also included in these experiments (at least very often), or to the nerve- and polarisation-current having passed simultaneously through the derivation-circuit.

In addition to this, the break-contractions before may be confounded with those after the hiatus, if the hiatus is short and does not appear at the same point when the main circuit is broken as when the nerve-circuit is broken. The fact that differences, even of a tenth of a second, in the duration of closure of the primary current affect the appearance of break-contractions very considerably should also be mentioned. I myself was once misled by this source of error through the one mercury key being less easy to manage than the other and so keeping the current closed a little longer. Finally, in comparative experiments the current ought not to be changed from a higher to a lower strength, and the long persistence of the polarisation-current must be kept in mind. All this is of importance for the attainment of accurate results. Although I by no means believe that Hermann neglected these facts and so fell into error, yet I am convinced that in his experiments the nerve- and polarisation-current have been intermingled, or have acted simultaneously. Otherwise he would not, if I may so say, have written so hesitatingly: 'When the break-contraction is struggling for existence it appears, if there is any difference at all,' &c. What I described was not a struggle: in a very large number of experiments, which I have considerably increased since the appearance of Hermann's paper, the break-contraction appeared much sooner after opening the main circuit than after opening the nerve-circuit.

The difference becomes much greater (as is seen in the experiments at page 108) if ordinary metallic electrodes are substituted for unpolarisable electrodes. The internal and external polarisation-

currents are conducted much better through the closed derivation-circuit than through the nerve itself. This experiment, which has been already described by du Bois-Reymond, shows how great an influence the polarisation-current (in this case chiefly external) exerts on the appearance of break-contractions [1]. But even with unpolarisable electrodes, and therefore with an internal polarisation-current only, the same thing occurs, though not to the same extent. Thus the less the resistance to the polarisation-current the more readily do break-contractions occur. These I shall call 'polarisation break-contractions,' in contrast to the 'additive' break-contractions previously referred to.

In conclusion, I shall shortly refer to a break-contraction which differs from that already mentioned in that its appearance is retarded. In my preliminary communication I regarded this phenomenon, which had been observed by Pflüger and was recently studied more thoroughly by Biedermann, as due to the fact that the anode of the polarisation after-current lay between the point of stimulation and the muscle, and hindered for a shorter or longer time (for the strength of the polarisation-current rapidly diminishes) the excitation from reaching the muscle. This explanation applies of course only to the case of opening descending currents, with which Pflüger had also exclusively observed this phenomenon. My experiments on this subject are however as yet incomplete, therefore I shall not give an account of them at present.

Apart from this retarded break-contraction, we have met with three distinct kinds of break-contraction in this investigation: (1) additive in the same direction; (2) additive in the opposite direction, due to the appearance of the nerve-current; and (3) polarisation break-contractions, due to the appearance of the current of internal polarisation. All these break-contractions can, as we have seen, be shown to be caused by, or, to speak more cautiously, to be coincident with the appearance of a new current rather than the disappearance of the original one. They may all therefore be in reality make-contractions. At any rate, we know with absolute certainty that closure of a current passing through a muscle or nerve excites these organs: when we see, on the other hand, that on opening a current a new current comes into existence, we are justified in inferring that it is the coming into existence of the

[1] This meets the objection in Hermann's paper, p. 105. He inferred from my preliminary communication that I had only used polarisable electrodes in my experiments.

latter, and not the disappearance of the former, that excites. In accordance with this inference, I should express as follows the law according to which currents excite a nerve or muscle :—

1. *A nerve or a muscle is excited by the coming into existence of a current through it.* The height of current-strength and the rapidity with which this height is attained are of account, in that the excitation increases with them up to a certain limit.

2. *A muscle or a nerve is also excited, though to a less extent, by a current flowing through it at a constant strength*[1]. For muscle this is known; for sensory nerves and the dilating vascular nerves of the skin I have demonstrated it[2]; that it is also true for motor and secretory nerves follows if we assume that all nerves are similar, or at least not very different, even though we may not be able to demonstrate excitatory effects in the end-organs of these nerves: for the reaction of the end-organs depends on conditions inherent in themselves, and on other factors not affected by excitation of a nerve. Moreover, Pflüger[3] and von Bezold[4] long ago asserted that under certain circumstances motor nerves react to a current of constant strength.

3. On the other hand, *a nerve or muscle is not excited by the disappearance of a current from it* (at any rate this has not been proved). The excitations observable on opening exciting currents correspond with the coming into existence of other currents (muscle- or nerve-currents or polarisation after-currents), and it is to this that the excitatory action is due.

4. *The direction of the exciting current, provided only that it be parallel to the axis of currentless nerves or muscles, does not appreciably affect the strength of the excitation of these organs themselves.* In the case of a nerve, however, the effect on its end-organ is of course modified if at make of a strong ascending current its anode, or if at break of a descending current the anode of the negative polarisation-current lies in the way and obstructs the passage of the excitation. I agree with Tigerstedt in distinguishing two strengths of stimulus here, namely, weak currents, at whose closure the excitation at the

[1] Strictly speaking, no currents—at least, no currents of short duration, such as are commonly employed for stimulation—flow through a nerve or muscle at a constant strength. For since both organs are polarisable there must occur in the first moments after closure an increase of current strength from positive, and immediately afterwards a decrease from negative polarisation.

[2] Pflüger's Archiv, xvii. p. 215.

[3] Elektrotonus, p. 453.

[4] Untersuchungen über die elektrische Erregung, Leipzig, 1861, p. 325.

negative pole overcomes the obstruction at the positive, and strong current, at whose closure the excitation at the negative pole is entirely blocked by the obstruction at the positive[1].

When muscle- or nerve-currents exist, the direction of the exciting current is not indifferent. In this case, closure of a current in the same direction has far more effect than closure of one in an opposite direction.

It still remains to consider some objections which may be made, and which have partly already been made, to these laws, and in particular to the third.

Hermann comes forward with the objection that he can see no reason for thinking that of two events like in kind—the coming into existence and the disappearance of a current—only the first should produce an effect.

But according to Hermann's own conception, the coming into existence and the disappearance of a current, in so far as these act as stimuli, are by no means events like in kind; for it cannot be assumed that the coming into existence of catelectrotonus is an event like in kind to the disappearance of anelectrotonus. But according to my conception, the coming into existence and disappearance of a current are like events as regards the way in which they act as stimuli. For with the disappearance of a current there is always associated the coming into existence of a new current, which causes the stimulus. Here there is in both cases a coming into existence of catelectrotonus, so that the two events are clearly absolutely alike in kind, which cannot be said of the other two. For the movement of a body away from its position of equilibrium is not to be assumed without some reason to be an event like in kind to its movement into that position, even if both movements are in the same direction. But according to my conception, only movement away from the position of equilibrium—the coming into existence of catelectrotonus—has an excitatory effect, not the return to that position—disappearance of anelectrotonus.

I cannot at present call to mind any state the disappearance of which acts as a stimulus on our organism; though a large number occur to me which do so at the moment of their coming into existence and during their continuance. The electric current

[1] It is not necessary to consider the effects of exceedingly strong currents, which Hermann (*loc. cit.* p. 103) has described under the title of the over-maximal phase of the law of contraction; for in this case, as Hermann has already said, there is only an apparent contradiction of the acknowledged facts of the law of contraction.

may now be placed side by side with these agents; it differs from them only apparently, since its disappearance only excites when accompanied by a reappearance of the stimulus. Nerve behaves to a current in some respects like an elastic body; it is not merely disturbed from its equilibrium on closure, but on opening overshoots its position of equilibrium in returning, before finally coming to rest. It is in this sense that I understand the almost prophetic sayings of Volta and Ritter in connection with this subject.

Volta[1] imagined that on breaking the conducting circuit an obstacle is suddenly presented to the electric current, against which it strikes, and rebounding gives rise to *a wave in the opposite direction.* Ritter[2], on the other hand, said that the make-stimulus is imparted to us, while we ourselves impart the break-stimulus. Ritter's words are: 'We have said that the phenomena occurring on opening the circuit of a galvanic battery form a subject of particular importance. We have now to justify this statement, and do so by drawing attention to the great fact that these phenomena occur at the moment when the organic body and its parts are withdrawn from the influence of the battery. They can in no way however be due to a direct action of the battery; for how could the battery produce such an effect when it is no longer present? The organism which was in its circuit must itself produce the effect, and can only do so in virtue of having been in the circuit, for apart from this there would have been no effect produced.' If Pflüger concludes from these words that 'Ritter imagined that a special state produced by the current disappears, which disappearance is accompanied by a contraction, as is every disturbance of the internal equilibrium of the nerve,' I cannot infer the same from Ritter's words; for on the disappearance of the current there might just as well reappear a state which had been kept in abeyance by the passage of the current, and act as a stimulus in reappearing.

Hermann goes on to make the further objection: 'But what seems to me more important is, that if we accept this conception we abandon the advance of most importance embodied in Pflüger's law, the acknowledgment, namely, that the excitation is due, not to the current itself, but to a definite change of state produced by it in the nerve-electrotonus, as expressly stated in Pflüger's enunciation.'

[1] Du Bois-Reymond, Untersuchungen über thierische Elektricität, Bd. i. p. 314.
[2] Gilbert's Annalen, 1801, xxiii. p. 30, quoted by Pflüger, Elektrotonus, p. 74.

To this I have a double answer. If by experiments and reflection any one reaches a new conception of a complicated process, he has no time to enquire whether his new view is in agreement with older views of the same subject. He has only to ask whether his view is in agreement with the *facts*. Though the older view may have brought into harmony a whole series of diverse phenomena in the most simple and complete manner, it may yet perhaps be erroneous, and, however dearly won, have to be abandoned and to make way for the others, as has more than once occurred in the history of science. A new theory, therefore, cannot be rejected for the mere reason that it is not entirely in agreement with old ones.

But in the second place I do not at all see in what way Pflüger's fundamental law, that the excitation is due not to the current itself but to a definite change of state produced by it in the nerve—electrotonus—is abandoned on my theory. For, according to my view just as much as according to that of Pflüger, the appearance of catelectrotonus acts as a stimulus; for Pflüger it is in addition the stronger stimulus; while the disappearance of anelectrotonus is for Pflüger the weaker, but for my theory no stimulus at all. The extremely important fact that the stimulus occurs at the cathode on closure, at the anode on opening, is however also explained by my theory. Besides, if with this fact we often proceed to associate the assertion that the appearance of catelectrotonus and disappearance of anelectrotonus act as stimuli, this conclusion is justified only if it can be shown that nothing occurs on closure except the appearance of catelectrotonus, and nothing on opening except disappearance of anelectrotonus. But if it be shown that on opening catelectrotonus appears in addition to anelectrotonus disappearing, the former being an event which is known to act as a stimulus, while it is not known whether the latter also does so, the assumption that in both cases the same cause produces the effect is the more probable and logical. Time will decide whether my theory constitutes an advance or not. The conditions are certainly not made to appear more complicated by it; it acknowledges only one part of Pfluger's law of excitation, and, so far at least as I can see, does not essentially contradict it. A nerve is excited only if it is moved from its position of equilibrium in a certain direction; on returning it is not excited. By this return it changes in the one case from a structure of increased, in the other case from one of diminished excitability to one of

normal excitability; but neither of these two events alone acts as a stimulus.

Further on Hermann refers, quoting experiments by Hering and Biedermann, to a series of phenomena from which he attempts to show that my theory is arbitrary, inasmuch as certain excitations can be regarded either as make- or break-excitations. This I fully admit, but would remark that no conclusion can be drawn from such experiments, either for or against any theory. I shall therefore not consider these experiments further.

But I must refer more particularly to one point, which is essentially of great significance for my theory, and has been brought forward in objection both by myself and by Hermann. It is well known that an opening excitation occurs, not only when the whole exciting current is opened, but also on disappearance of a portion of it. In the first case the stimulus was caused by the appearance of the polarisation-current; but can the same explanation be offered if part of the original exciting current remains? The accompanying diagrams will express the alterations in the current which occur in this case.

Let us suppose that a current of strength S passed along a nerve falls to zero at any moment t. According to the ordinary theory it is this fall which produces the excitation, but according to our theory it is the sudden appearance of the polarisation-current in the opposite direction which at its first appearance may have the same strength as the original current. If now instead of letting this current fall to zero (or, which is the essential point for us, instead of causing a polarisation-current equal to the original current but opposite in direction to appear) we let it fall to half its original strength, it is easy to see that according to the above assumption the polarisation-current will have, not the strength S, but only half the strength. [In other words, if the polarisation-current produced by the passage of an extraneous current S through a nerve is of such strength that they mutually mask each other, the effect of opening the extraneous current is to unmask a counter-current of which the initial intensity is equal to S. If S is not opened but merely diminished, the counter current will be similarly unmasked, but will have an initial intensity equal to the amount by which S has been diminished. In the original this is illustrated by a figure which we omit.—Editor.]

The first question, accordingly, which presents itself is as to the

strength of the polarisation-current at its first appearance as compared with the strength of the original current. Is the strength of the former equal to, smaller, or greater than that of the latter? I am unfortunately not in a position to give any definite reply to this question. If, however, we reflect that a nerve is an organ which possesses in a high degree the capability of being polarised, if further we call to mind the relative values which du Bois-Reymond[1] and others[2] have found for the strengths of the original and polarisation-currents, it will not seem too high a value if we assume that the polarisation-current is equal in strength to the original current.

If, however, this question must for the present be left unanswered, there is a second question which can be decided by experiment. This second question is: To what fraction of its original strength must an exciting current fall in order that an excitation of a nerve and muscle, a so-called 'incomplete' break-contraction, may occur? The way in which this question may be settled is simple. It is only necessary to arrange a mercury key *A* (see Fig.) in the course of the wire of the compensator *DD'* and best close to the point *D*, where the current divides. A second mercury key *C* is placed in the main circuit *DD'B*. If the main circuit is closed at *C* while the derivation-circuit is open, the whole current from the battery *B* passes through the nerve; and if the key *A* in the derivation-circuit is now closed also, the current falls to a certain fraction of its strength, which fraction is of course the smaller the smaller the distance between *D* and *D''*. The current strength could thus be altered from *S* to any strength between *o* and $\frac{3}{4}$ *S*.

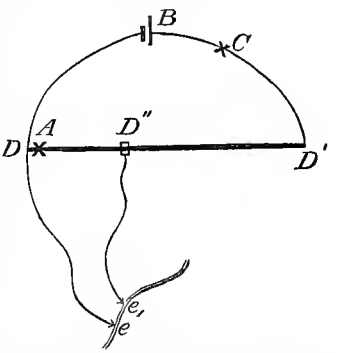

Fig. 1. Main or battery circuit *BCD'D*. Derivations or nerve circuit *Dee,D''*.

The most remarkable fact which we observed was that the direction of the original current has a most important influence on the appearance of imperfect break-contractions. It was found as mean of a large number of experiments that an ascending current of the strength of one Daniell, which was of course led

[1] Ges. Abhandlungen, i. p. 43.

[2] See Wiedemann, Electricitätslehre.

to a currentless piece of nerve through unpolarisable electrodes, must fall to about 0·6 of its whole strength in order to produce an imperfect break-contraction. A descending current, on the other hand, must fall to at least 0·3 of its original strength to produce a similar excitation. Often, however, after frequent repetition of the second experiment no contraction at all occurs, even though the descending current is reduced to zero.

The following experiment will serve as an example:—

EXPERIMENT.—Nerve-muscle preparation of a grass-frog of medium size in the moist chamber of the myograph. Unpolarisable electrodes about 7 mm. apart, the distal one about 1 cm. from the muscle, at an indifference-point. Very weak ascending and descending currents produce equally strong contractions. With key *A* open key *B* is closed, and key *A* is afterwards closed regularly after an interval of a second, followed by opening of *B*, while *A* remains closed. The first weak imperfect break-contraction with gradually increasing falls of current-strength occurs with $DD''=$ 250 cm., and increases in size regularly until DD'' nearly $= 0$. The current was ascending, one Daniell being used. A current with $DD''=250$ cm. corresponds to 0·62 of the original current. It is of importance that in each experiment, whether a contraction is produced or not, the key *A* should remain closed for a short time, in order to get rid of the polarisation-currents. If this is overlooked the results become uncertain and inconstant, so that an imperfect break-contraction first appears at a different point if the current-strengths are altered in the opposite direction, i.e. if the current is first made to fall to zero, and the succeeding falls are made less and less; in other words, if the distance DD'' is gradually increased from its minimum.

The following fact is also worth mentioning. With plain metallic electrodes of copper, which give a strong polarisation-current, if key *B* remain open and key *A* be repeatedly closed, several successive contractions, diminishing in size, may often occur. These are caused by the polarisation-current in the nerve, which thus does not disappear very rapidly, and passes at each closure of *A* without entirely exhausting itself. It is therefore of great importance to keep the key *A* closed for a few seconds after each experiment; the results then become perfectly constant.

With an ascending current, on the other hand, the first imperfect break-contraction occurs with $DD''=100$ cm., or sometimes not till $DD''=40$ cm., that is to say, with a reduction of current to about 0·22 or 0·1 of its original strength. On further repetition of the same experiment, or with other nerves, no imperfect break-contraction may occur, even on reduction to zero.

Let us try to explain these results on Hermann's theory that the stimulation in the case of imperfect break-contractions always occurs at the anode of the exciting current, and that there is no reversal of the direction of the exciting current. In the case of an ascending current the stimulation would occur at the anode next the muscle, and would have to traverse a more or less considerable extrapolar tract of anelectrotonic nerve in order to reach the muscle. It would thus reach the muscle diminished in strength according to the prevalent view, which may be considered to be firmly established by the experiments of Pflüger and by Tigerstedt's recent researches. With a descending current the

stimulation, according to Hermann, would again occur at the anode, which however is now furthest from the muscle. In this case the excitation, which may be made of the same strength as in the previous case, has now likewise an anodic (intrapolar) tract to traverse, but soon reaches the catelectronic region, which it does not again leave, even when it has passed the neighbourhood of the cathode. This excitation would therefore reach the muscle, not diminished, but increased in intensity; for it follows from the earlier, but particularly from the exceedingly valuable recent re-rearches of Tigerstedt, that an excitation always increases in intensity in passing the cathode or the catelectrotonic region of a nerve. With a descending current therefore the excitation at the anode would reach the muscle reinforced, with ascending currents it would do so diminished in strength. In other words, the imperfect break-contraction would appear in the case of a descending current with a small fall of current-strength: with ascending currents, on the other hand, only with a much larger fall; for the former weak excitation would be reinforced in passing the cathode, while the latter stronger one would be weakened in passing along an anodic tract.

But we see that exactly the opposite actually occurs of what would occur if Hermann's theory were true. Ascending currents have only to be slightly, but descending currents very greatly diminished in strength to produce an imperfect break-contraction. This result is readily intelligible according to our theory; for the conditions for an imperfect break-contraction are nearly the same as for a complete break-contraction. That is to say, a reversal of the current occurs, and at opening of descending exciting currents the anode of the polarisation after-current intervenes between the point of stimulation and the muscle, while at opening of ascending exciting currents the cathode (at which excitation occurs in every case) of the polarisation after-current is next the nerve.

Hermann[1] will no doubt object to my argument that he can explain all the above results by means of his theory of polarisation increment. For at opening of ascending currents the excitation would occur at the anode and pass to less positive parts of the nerve, while at opening of descending currents the excitation, starting likewise from a point whose polarisation is strongly positive, would pass into parts negatively polarised. In the first

[1] See Hermann, Handbuch der Physiologie, ii. part i. p. 165, and Pflüger's Archiv, vi. p. 359.

case the excitation would be reinforced, in the second weakened. But I can scarcely believe that Hermann will still maintain this theory of polarisation-increment now that Tigerstedt[1] has clearly shown by unimpeachable methods that an excitation which has to pass the cathode is never weakened, but always reinforced, and that the theory of polarisation-increment is therefore incorrect.

I come now to an additional point which is of importance in explaining the imperfect break-excitation: this concerns the time during which the whole current passes along the nerve before being reduced to a fraction of its strength. Since a nerve is an organ which becomes strongly polarised, it is intelligible, and has besides been directly demonstrated by du Bois-Reymond[2], that a constant current passing through a nerve is weakened by internal polarisation, and, within certain limits, is the more weakened the longer it passes. Although in the latter case the exciting current has already diminished in strength when it is suddenly diminished to a fraction of its height, the fall is no greater than in the case in which there has been no previous diminution. Consequently the same amount of anelectrotonus would disappear in each case, and if this disappearance of anelectrotonus caused the excitation, the fact that differences in the duration of closure affect the break-contraction, which they do very considerably, would be unintelligible[3]. The duration of closure has just as much influence on the appearance of the incomplete break-contraction as it has on that of the complete break-contraction. The longer the current remains closed, the earlier do they both appear. That is to say, with a long closure the imperfect break-contraction appears with quite a small fall as compared with that which is necessary with a short closure. According to Hermann's theory this is not intelligible, but according to ours it is readily so. For with a longer closure the polarisation-current which is unmasked is stronger than with a shorter closure.

The duration of closure varied in our experiments between ½, 1, and 2 seconds, and the results in each case were in accordance with theory.

A few words in conclusion as to the influence of current-strength on the appearance of imperfect break-contractions. It

[1] Above, pp. 20, 21.

[2] Gesammelte Abhandlungen, ii. p. 256.

[3] This reasoning of course applies also to the case of the complete break-contraction.

[4] [In the original this statement is illustrated by a diagram. ED.]

is easy to observe, for both ascending and descending currents, that within the current-strengths used by us ($\frac{1}{10}$ Daniell to about 7 Daniells) imperfect break-contractions appear the earlier the stronger the currents are. Thus with a strong current excitation is caused by a fall of a smaller fraction of its height than is necessary with a weaker one. (I shall not give detailed numbers here, since these facts are only mentioned for the sake of completeness. They can be as well explained by Hermann's theory as by ours). For if a current of strength S is allowed to fall a half, it produces the polarisation-current of which the initial strength is half S; whereas a current of half the strength similarly allowed to fall a half gives only a current of a quarter S. The first current has not therefore to fall a half in order to produce the same effect as is produced by the second when suddenly diminished in the same proportion. This fact is however evidently also in accordance with Hermann's theory; for in the one case there is a fall of current-strength of $\frac{H}{2}$, in the second of $\frac{H}{4}$. For producing weak electromotive forces we used a Noë's Thermopyle, the flame of which was placed at different distances from its middle.

As the reader will now see, the results of all these experiments on the imperfect break-contraction are not only intelligible on our theory, but present almost insuperable difficulties to the ordinary explanation. For the present I can see no single objection which can be brought against my own and Tigerstedt's conception of the nature of the break-excitation. Of course I shall not persist in my opinion if any one can prove to me that the *mere* disappearance of anelectrotonus produces excitation. In any case no one can deny that I have referred about 80 per cent. of all so-called break-excitations to make-excitations, and that the polarisation after-current has great significance as regards the causation of the remaining 20 per cent., as even Hermann acknowledges. But it is more than probable, and to me it seems certain, that the polarisation-current is the sole cause. I must, however, add that it would have been desirable if I could have directly proved this by experiment for the incomplete break-excitation. The experiment would require to be arranged so that when the fall of current-strength that first produced an incomplete break-excitation was reached, the current passing through the derivation-circuit $DAD''e'e$ should be immediately led to a galvanometer. This current must then be in the opposite direction to that of the

original exciting current, provided that the whole of the fibres of a nerve-trunk give as strong a polarisation-current as those whose excitation we observed in the case of the gastrocnemius, which is not altogether certain. Unfortunately I do not possess the apparatus necessary for this experiment, and I must ask the reader to be content for the present with the evidence which I have been able to bring forward.

V.

ON NERVE-EXCITATION

BY THE

NERVE-CURRENT.

By EWALD HERING,

Professor of Physiology in the University of Prague.

Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Vienna, vol. lxxxv. Part 3, p. 237. 1882.

V.

At the end of my communication[1] on the direct excitation of muscle by the muscle-current, I promised to communicate analogous observations on nerves, and to prove that the excitation of nerves by the nerve-current occurs more frequently and is more easily accomplished than has been hitherto supposed. But in the winter of 1879 the frogs at my disposal suddenly became unfit for such experiments, and I was obliged to interrupt them.

Since then Kühne[2] has communicated observations on the excitation of nerve by its own current, which I shall have occasion to confirm in the following pages. My researches, however, in many respects go beyond those of Kühne, especially in this, that I have succeeded in eliciting from nerves a true secondary contraction and secondary tetanus, which neither du Bois-Reymond nor Kühne held to be possible, and I have so definitely learned the conditions necessary to the success of these experiments, that they will henceforth be easily and successfully repeated by anyone.

1. Excitation of the Nerve by its own current.

Du Bois-Reymond's Experiment.

As is well-known, du Bois-Reymond showed that it is possible to excite, by means of its own current, a nerve which is provided with a transverse section. Placing the sciatic, separated from its centre, and in connection with its muscles, so that transverse and longitudinal sections respectively were in contact with the cushions

[1] Sitzungsberichte, lxxix. 3. p. 7.

[2] Untersuch. aus d. physiol. Inst. zu Heidelberg, iii. p. 90, 1879.

of his electrodes of the old form covered with films of albumen (which had been previously tested by the multiplier and found to be free from polarity), he made and broke the nerve-current by means of a mercury key. 'The leg contracted at closure, and often at opening; in a few cases it contracted at opening only[1].'

Later, du Bois-Reymond simplified the experiment by dispensing with all metallic conductors; he placed two conducting cushions, separated by an interval of a few mm. on a non-conducting support, then laid the nerve upon the two cushions with transverse section upon one cushion, longitudinal surface on the other; then, by means of a third cushion he completed the circuit, thus closing the nerve-current[2]. Since this method allows of a rapid closure of the current by the sudden application of the third cushion, but of a less rapid opening by its removal, it is advisable to arrange the two cushions upon which the nerve rests so as to overhang the edge of a glass plate; a vessel filled with salt-solution can then be raised quickly, so that the overhanging tips of the cushions suddenly dip into the fluid; or it can be quickly lowered, so as to break the nerve-current suddenly.

Instead of the cushions, one may use blocks of saline clay, which have the advantage that they may be modelled to any desired shape. This is the method which Kühne has preferred, and which I also have frequently used. I kneaded the clay with concentrated salt-solution, and used the same material to complete the circuit; in order to protect the nerve from the action of the concentrated salt-solution, I placed upon the spots, where the nerve was to lie, a thin layer of clay, made with salt-solution 0·6%, or a bit of blotting-paper moistened with the same. If sufficiently excitable nerves are to be had, 0·6 % solution may be used both in preparing the blocks, and for closing the circuit. The contractions which one obtains in this manner are, as Kühne also states, very energetic in favourable cases. The opening contractions are generally weaker, or do not occur at all; sometimes, however, they are strong, as indeed has already been stated by Kühne. I may also confirm the statement of du Bois-Reymond to the effect that sometimes an opening contraction alone appears.

In all cases where it is desired to compare make- with break-contractions, or make-contractions taken with different lengths of the interpolar region, it is advisable to employ du Bois-Reymond's

[1] Unters. über thier. Elektr. ii. p. 273, 1849.
[2] Fortschritte d. Physik. iv. Jahrg. p. 314, 1852.

original method by metallic closure of the circuit, and to make use of some arrangement providing for equal rapidity of closure and opening. And with this one must naturally be most careful as to the electrical uniformity of the unpolarisable electrodes, since any nerve that will react to its own current, will also be extraordinarily sensitive to the weakest additional current, if the latter should be in the same direction as the former in the interpolar region. Closure, by means of a liquid or by a conducting cushion, cannot, at any rate by hand, be performed with sufficient uniformity, and if the contractions are not very strong, one obtains, in spite of the greatest practicable uniformity of speed in raising and lowering the liquid which completes the circuit, a succession of contractions of very different strengths.

Excitable preparations gave me strong make- and break-contractions even when the portion of nerve between the blocks of clay was as much as one centimeter long, and in one case I still obtained make-contractions when it reached a length of 25 millimeters. I have not closely examined the conditions of the appearance or predominance of the break-contraction.

I must not, however, omit to mention that *this break-contraction, if one admits certain assumptions concerning the so-called internal closure of the nerve-current, is to be regarded, not as a proper 'opening-contraction, but as a contraction due to the closing of the nerve-current.*

Since it is possible, in the above-described manner, to obtain on a single preparation a long series of closing- and opening-contractions, all that is necessary in order to tetanise the nerve is to make the closures and openings succeed one another with sufficient rapidity just as in the case of a battery-current. Kühne used for this purpose a vibrating mercury key. I have considered it advisable to avoid the use of any metal in this experiment, partly in order to dispense with the testing of electrodes by the galvanometer, partly in order to demonstrate a 'tetanus without metals.' To this end I fixed the cushion which serves to complete the circuit in du Bois-Reymond's experiment, to the end of a rod which could be made to vibrate, so that the cushion could, just like the hammer of Heidenhain's tetanomotor, be applied to and removed from the blocks of clay in a rapid rhythm. At first, I used for this purpose a large Neef's hammer, which sometimes gave me a very strong tetanus, but often failed, because the amplitude of movement of the cushion was too small, so that threads of fluid between it and the blocks of clay prevented the circuit from being broken. I eventually

used a little apparatus, specially constructed for the purpose, which I propose to call a *tetanomotor for the production of tetanus without metals*. In this apparatus the rapid raising and lowering of the cushion is effected as follows: The teeth of a toothed wheel raise a lever, to the free end of which the cushion is attached, and a spring depresses the lever after each elevation; by means of a screw the amplitude of movement can be exactly regulated, and by varying the rapidity of revolution of the toothed wheel the frequency of the makes and breaks may be varied.

Excitation of a nerve by its fall upon a moist conductor.

The easiest way to effect an excitation of nerve by its own current is to let its end fall upon some currentless moist conductor. It is less advisable to let it fall on platinum or amalgamated zinc, partly on account of the instantaneous polarisation, partly on account of the admixture of currents due to electrical differences at the points of metal with which the nerve is in contact. The possibility of mechanical excitation, which can only occur when the nerve is too dry, is easily excluded by control-experiments with non-conductors.

The fall of the end of a nerve upon a drop of lymph, serum, or normal salt-solution, is, in general, successful only once, because, on removal of the nerve, the adherent fluid permanently short circuits the current, but the experiment can be repeated several times if the nerve is allowed to fall upon a coagulated drop of blood, or a block of clay made with salt-solution ·6 p.c.

It need hardly be explained, after what has been said, that a contraction follows also if the end of nerve is dropped upon a completely currentless muscle or any other currentless organ. If one drops the sciatic nerve left in connection with the leg-muscles upon these muscles in the ordinary way, the consequent contraction is by no means a sufficient proof that the nerve has been excited by a muscle-current, although indeed this will generally be the case. In this favourite but not at all unequivocal experiment, the contraction may be due to any one of three causes if the leg has been stripped of its skin: either (1) that the leg gives an ascending current sufficient for excitation, which traverses the nerve from its point of entrance into the muscle to the point where it is in contact with the muscles of the leg, or (2) that the nerve lies upon electrically different points of muscle, or (3) that the nerve-current is suddenly closed through the muscle. It is easy to understand that in most cases all three factors may concur or conflict with one another.

Czermak found[1] 'that a current-testing frog's limb gives a closing contraction, if its nerve is raised on a glass rod and suddenly dropped upon the natural longitudinal section of a rabbit's or pigeon's muscle, which happens to be in partial idio-muscular contraction, so that it is simultaneously in contact with a contracted and a non-contracted portion of such muscle.' He remarks also that 'very excitable frog's limbs' likewise contract if their nerves fall upon an unaltered natural longitudinal section of the muscle, and he explains this by the assumption that there are weak currents between different points of such a surface. But Czermak found also that frogs' legs of the highest degree of excitability gave distinct and even very strong contractions if he let their nerves fall upon a quiescent portion of a rabbit's intestine, or upon the kidney or liver of the same animal. To infer from such contractions that there is current from these tissues is not admissible, until it has been shown by adequate control experiments that the nerve does not react, to the closure of its own current.

Kühne[2] has already called attention to the fact that Donders was mistaken in regarding, as an effect of currents from the cardiac muscle, the contractions of the frog's leg which may be obtained by dropping its nerve on the pericardium during the cardiac pause, and he has shown that similar contractions may be obtained when the nerve is dropped on to the pericardium after the heart has been removed.

Interference between a nerve-current and a battery-current.

The effects of electrical excitation of a nerve in the vicinity of its transverse section depend so much upon the nerve-current which is present as to be quite unintelligible if this current is not taken into account.

According to the report of the fifty-fourth meeting of German savants at Salzburg, Grützner has recently called attention to the paramount importance of the nerve-current to the excitability of the nerve, or of any other nerve lying in contact with it—a consideration which is already, to some extent, suggested by Pflüger's 'Researches on Electrotonus[3].'

He says[4], 'As conducing to the effect of excitation with constant

[1] Über secundäre Zuckung von theilweise gereizten Muskeln aus Sitzungsberichte dieser Akad. 1857, und Gesammelte Schriften, i. p. 429, Leipzig, 1879.

[2] *Loc. cit.* p. 85. [3] p. 151. [4] *Loc. cit.* p. 119.

or with induction currents, the currents of the nerve itself are of great importance, especially such as can be shown to exist in the neighbourhood of the section or of branches, as well as in that of the physiological terminations peripheral and central—such currents adding themselves algebraically to the exciting currents, and so increasing or diminishing them. In this wise are explained the statements concerning the differences of excitability at different points in the course of a nerve-trunk, as well as the varying results of excitation with weak currents.'

Since a more detailed account may be expected from Grützner at some future time, I will here confine myself to the record of a particular instance which belongs to this class of phenomena, and which is of interest because a contraction actually caused by closure of a derived nerve-current appears as if caused by opening of a weak battery-current, and conversely a contraction caused by opening of a branch of a nerve-current appears as if due to closure of a weak battery-current; a case then *in which, as a matter of fact, a make-contraction may be mistaken for a break-contraction, and vice versa.*

Assuming that a rheochord is used to send by derivation a fraction of a battery-current through the nerve, and that the key is introduced between the rheochord and the *unpolarisable electrodes*, then, if the nerve is in contact with the electrodes by a transverse and by a longitudinal surface, the key will short-circuit the nerve-current, and possibly a contraction will ensue, even when the rheochord is not in connection with the battery.

Under similar conditions, but more seldom, there may be a contraction when one opens the nerve-rheochord circuit, or, as I shall term it, 'nerve-circuit.' For this to happen it is necessary to choose a preparation which, under the above conditions, gives break- as well as make-contraction with its nerve-current.

If now the rheochord is connected with the battery, so that the derived current is ascending in the nerve, this current will be opposed to the nerve-current in the nerve-circuit, and may compensate it exactly if of appropriate strength[1], which particular case we will now assume. The consequence will be that closure of the nerve-circuit will no longer give any contraction, because, in spite of the closure in the conductors between nerve and rheochord, no

[1] I need hardly remark that I speak here of compensation of the nerve-current not in any absolute sense, but only in accordance with the conventional sense of the word. For there is no question here of a true compensation of current in the nerve, but only of a compensation of the branch current in the conductors which connect the nerve and rheochord.

new current comes into existence whether as a branch of the battery-current or of the nerve-current, and consequently no electrical change of the nerve. Nor can there be a contraction at opening of the nerve-circuit, although such was present in the absence of the battery-current.

The preparation will act quite differently if a key is placed between battery and rheochord—in the 'battery-circuit' as I shall henceforth designate it for the sake of brevity. If the latter is closed subsequently to closure of the nerve-circuit, this will be equivalent, as regards the nerve, to opening of the nerve-current, and the muscle will contract. And now *what appears to be the closure effect of a current derived from the battery, is, in reality, the effect of breaking the nerve-current*[1]. Under such conditions then a contraction is obtained if with previously closed nerve-circuit the battery-circuit is closed; but, on the contrary, no contraction if with previously closed battery-circuit the nerve-circuit is closed.

If when both circuits are closed the key of the battery-circuit is opened, the compensation of the nerve-current in the nerve-circuit is removed, and the muscle contracts because the nerve-current is at the same time reclosed. Thus, what now appears to be an opening effect of the derived current of the battery, is, in reality, a closure effect of the nerve-current, so that under the conditions in question a contraction is obtained if, after previous closure of both circuits, the battery-circuit is opened; but, on the contrary, no contraction if the nerve-circuit is opened.

If the branch current from the battery is too weak to compensate the nerve-current in the nerve-circuit, its effects will manifest themselves in the same direction as above, but not in the same degree. If, on the other hand, it is somewhat stronger than is required for compensation, the nerve will, with the closure of both circuits, be traversed by an ascending current—a remainder, so to speak, of the branch current of the battery. And if the nerve-circuit is closed after previous closure of the battery-circuit, there is no contraction, provided the branch current of the battery does not exceed a certain strength; if, on the other hand, the battery-circuit is closed after previous closure of the nerve-circuit, the opening effect of the nerve-current adds itself to the weak, and of itself inadequate, closure-effect of the branch current of the battery, and

[1] That under certain conditions the break-contraction due to the nerve-current must in reality be considered as a new make-contraction by the nerve-current, has already been mentioned on p. 129.

a contraction is obtained. If with previously closed battery-circuit the nerve-circuit is opened, there is no contraction, assuming always that the ascending battery-current in the nerve is not so strong as to give an opening contraction in spite of its partial compensation by the nerve-current. If, on the other hand, with previously closed nerve-circuit the battery-circuit is opened, the nerve-current finds by this closure, a new channel of derivation, and a contraction follows, which is, in this case, further strengthened by the influence of the voltaic alternative. Then, if we may assume that this is due to the circumstance that a spot at which a current enters becomes more excitable to a current which makes its exit by it, the closing excitation of the nerve-current will thereby be rendered all the stronger. As to the influence which may be exerted by polarisation currents, I will here entirely pass it over, since such currents are also closed in the nerve-circuit whenever the battery-circuit is opened.

All the above-mentioned circumstances must be taken into account, if the preparation does not give any contraction to simple closure or opening of the nerve-circuit in the absence of any battery-current. For, in this case also, the nerve-current is present, and its influence manifests itself in the same direction.

One thus obtains, with the weakest branch currents from the battery provided that they leave the nerve by its transverse section, an 'opening contraction' first at opening of the battery-circuit, and only with considerably stronger currents at opening of the nerve-circuit; and in correspondence with this a 'closure contraction' shows itself, first at closure of the battery-circuit, and only with stronger currents at closure of the nerve-circuit.

Up to this point we have assumed that the weak branch-current from the battery leaves the nerve by its transverse section. In the opposite case the consequence will be different according as the battery-circuit is closed after previous closure of the nerve-circuit, or *vice versa*. For, in the former case, a current—that of the nerve namely—already enters by the electrode which is in contact with the longitudinal surface, and this current will simply be increased by the additional branch current of the battery. But if the nerve-circuit is not closed until after the battery-circuit has been closed, the nerve- and battery-currents add themselves together at the moment of closure, and consequently the effect of such closure will be greater. Similarly, by opening the nerve-circuit both currents are simultaneously broken.

As a matter of fact, beginning with the weakest currents entering the nerve by its transverse section, one first obtains the make-contraction at closure of the nerve-circuit, and only with stronger currents at closure of the battery-circuit as well. And similarly in the case of the break-contraction.

Biedermann[1] has recently examined the relative inefficiency of currents which pass out of a nerve at its transverse section; a phenomenon which he has found especially striking in the case of the nerves of warm-blooded animals. Concerning this matter one must be careful to distinguish, in a current that flows through the nerve, between such branches as have their course in the excitable substance of the nerve fibres from those which traverse constituents of the nerve which simply do duty as physical conductors, in other words, the physiologically important from the physiologically unessential. The points where any such physiologically important current enters or leaves the excitable substance of a nerve fibre are to be regarded as its physiological anode or kathode. If now a certain part of the proper nervous substance of a fibre is electromotive, as we may, according to Hermann, assume the part adjoining an artificial transverse section to be, and if the current arising at this spot is opposed in direction to any branch current from the battery, then it is clear that a passage of the latter through the electromotive portion of the fibre can only occur when the nerve-current which already exists at that spot is overcompensated by the current which is led in, this requiring, of course, a relatively strong battery-current. Supposing further that the electrical current excites the nerve only at its point of exit from the excitable substance, *then an excitation by a current leaving the nerve by a transverse section would not be possible unless this current were sufficient to overcompensate the nerve-current at its source.*

As to how far the current, once it has exceeded the local strength or density requisite to this internal compensation of the nerve-current, can act as an excitant to the electromotive portion of the nervous substance by means of its residue, so to speak, must for the present remain unanswered on account of the alteration of the nerve-substance which obtains here. Beyond this point the current no longer finds any excitable substance.

Similar considerations may be urged concerning the relative

[1] Beiträge zur allg. Nerven- und Muskelphysiologie, Sitzungsberichte, Vienna, vol. lxxxiii, Part iii, p. 289, 1881.

inefficacy of currents having their point of exit from muscle by an artificial transverse section—a fact which has also been pointed out by Biedermann.

I need hardly say that what has been advanced above stands or falls with the theoretical assumptions upon which it rests.

Concerning the liability of frogs kept in the cold to tetanic excitation.

The frogs which I used for my experiments had been kept for several months in a cellar, at a temperature of about 0°. Since, for each series of experiments, I used them immediately after they had been fetched from the cellar, or, at any rate, after they had been placed between a double window, at the temperature of 0°, these frogs showed, with few exceptions, the disposition to enter into tetanus which has already been remarked upon by Pflüger[1].

This was especially the case with regard to *Rana esculenta*; *Rana temporaria* was much less inclined to fall into tetanus. What I have to mention, therefore, relates in general to water-frogs; in experiments which were made on land-frogs, the fact is specially mentioned.

If I divided the spinal cord of a *R. esculenta* which had been kept in the cold (or, briefly expressed, a 'cooled frog'), tetanus very rarely supervened in the inferior extremities; but, on the other hand, it did so almost constantly if the incision through the spine was made so low as to affect the nerve-roots; and the same thing happened if I cut through the *sciatic plexus*. The strength of the tetanus was very variable; sometimes the limbs passed into a prolonged and steady rigidity, which then gradually relaxed through a stage of clonic spasms; sometimes the spasms were clonic from the first. Its duration was equally various, and occasionally reached as much as four minutes. As a rule, the spasmodic stage immediately followed the contractions caused by the incision, but sometimes several seconds elapsed after the cessation of these contractions—as many as six—before the preparation, which had become quite quiescent after the incision, began to twitch again. This was always a sign of a comparatively slight tendency towards tetanus.

I have made this remarkable tetanus after section of nerves (which was not mentioned by Pflüger, though it certainly must have been known to him as to other observers) the subject of

[1] Untersuch. über die Physiol. des Elektrotonus, p. 133.

special investigation, but I shall here mention only such points as bear on what follows.

To these belongs, in the first place, the fact that a second section, when the muscles have become quiescent, generally causes a renewal of the spasms, though they are as a rule weaker after each new section.

In the second place, it is to be remarked that the spasms are usually stronger and more lasting the higher the nerve has been cut. If I cut through simultaneously the sciatic plexus of one side, and on the other the sciatic nerve in the thigh or just above the knee, and then compared the spasms on both sides, after fixing the knee so as to prevent any movements caused by the muscles of the thigh, I found that the spasms were as a rule much weaker and shorter in the last named limb, and that occasionally they were quite absent even when the other side entered into active movements. But if only a few such experiments are made it may perhaps be found that this rule does hold good, for it is liable to many exceptions, the causes of which can only occasionally be assigned. Thus, for example, the neighbourhood of injured and therefore electromotive muscles may cause modifications. But in the large number of experiments I made, the rule in question came out quite clearly.

Preparations which gave strong tetanus by section of the nerves, often reacted with a tetanus previously to such section, to closure or opening, even when the battery-currents were only just strong enough to act. Simple twitches were less frequent, and appeared for the most part when the battery-current was closed several times in succession in the same direction; the first closure, for instance, giving closure tetanus; the second, clonic disturbance; the third, a simple twitch only. Reversal of the current then restored tetanus.

All this appeared in a still more striking manner if I cut the nerve, and applied the electrodes to the transverse and longitudinal sections. With descending currents, even the weakest, I then obtained a strong closure tetanus, and with ascending currents an equally strong opening tetanus. And preparations which did not respond by a tetanus to the section of their nerves, fell into a strong closure tetanus (provided they were taken from cooled frogs) as soon as I made a descending current, or broke an ascending current, having thus in the first case its point of entrance, in the second its point of exit, at the transverse section. In these experiments the unpolarisable electrodes were only from 2 to 3 mm. apart.

I have already mentioned that the land-frogs which I used showed much less disposition to tetanus after nerve-section than did water-frogs. I, however, obtained from the former also strong closure or opening tetanus by excitation of the transverse section.

Pflüger [1] has attempted to explain the great disposition of frogs brought from a cold to a warm place to fall into a tetanic state, by some 'transposition of atoms' brought about by the influence of warmth. But without any desire to call in question the influence of warmth on a preparation, I must mention that frogs which had been kept in a cold room gave a tetanus of the corresponding limb after section of the sciatic plexus, even when the section was made in the same cold room and with cold scissors, so that any warming of the preparation was out of the question. They also reacted tetanically to weak battery-currents.

The tetanus consequent upon nerve section can be completely arrested, or, at any rate, much diminished, by weak ascending currents, if one electrode is applied to the transverse section, and the other to a neighbouring point of the longitudinal section. It recommences, however, when the current is broken. A strong muscle-current suffices to arrest it. If I placed the recently cut nerve between two muscles possessing a transverse section, in such a way that the transverse sections of the nerve and of both muscles lay in the same plane, I observed that the tetanus forthwith diminished or entirely disappeared, reappearing after removal of the muscles. Thus it happens that, even with the most excitable frogs, the tetanus is generally absent if the whole thigh is severed at one blow of the scissors, because the currents of the cut muscles forthwith act upon the cut nerve.

If the sciatic nerve on one side is laid bare, and divided after careful isolation from the muscles, the leg, if the preparation is a sensitive one, becomes tetanised; while an incision on the other side, and at the same level, but passing through the nerve and all the muscles, causes a contraction of the leg only during the operation, and is followed by complete relaxation. If after section of the sciatic plexus a strong tetanus should have supervened in the leg of that side, it is at once abolished by sudden amputation through the thigh; but if thereafter the two branches of the sciatic nerve above the knee are divided, tetanic agitation of the leg reappears.

[1] Untersuch. über die Physiol. des Elektrotonus, p. 133, 1859.

Closure tetanus of the nerve by the agency of its own current.

The great liability of cooled frogs to tetanic excitation explains the fact that even the derivation or short circuiting of the nerve-current is sufficient in suitable preparations to cause a closure tetanus which in favourable cases may be lasting, and of such steadiness and energy as to be comparable to the tetanus produced by induction currents. In most cases, it is true, the tetanus is unsteady or clonic, and the derivation of the nerve-current often brings about only an irregular agitation of the muscles; in short, there are here manifested all those appearances which one may observe when the closure of a weak battery-current sent through the nerve causes an enduring excitation of the nerve, and not merely closure contractions.

Whichever of the above described methods of establishing derivation be used, there will always result in certain cases, with very excitable preparations, an enduring excitation of the nerve, sometimes after the first closure only, sometimes after repeated ones. This lasting excitation may show itself by weak, irregular, or even rhythmical movements of single parts, or by stronger clonic spasms, or finally by well marked stretching tetanus. If to the original tendency towards tetanic excitation there be added any drying of the nerve, a permanent closure tetanus appears all the more readily. If the preparation is capable of responding to derivation of its nerve-current by a lasting excitation, it is no longer so necessary to provide for the rapid closure of the derivation-circuit, because, even failing a closure contraction, the persistent excitation is still appreciable.

An observation belonging here is as follows: I allowed the end of a dependent nerve of a galvanoscopic frog's limb to dip into salt-solution 0·6 %. I then made above the level of the fluid, a kind of transverse section by crushing the nerve with fine forceps. I allowed the contractions caused by this proceeding to subside, and when the preparation had become quite quiescent, I gradually raised the vessel containing the salt-solution so that the nerve was immersed in it deeper and deeper. As soon as the surface of the fluid rose above the crushed part a tetanus of the preparation appeared, which became stronger as I continued to raise the vessel, and reached its maximum when the surface of the fluid was about 1 cm. above the crushed part. If I raised the vessel still higher, the tetanus diminished, without, however, entirely

disappearing. If I now lowered the vessel, the tetanus increased, and was again at its maximum when the surface of the fluid was 1 cm. above the injured part. Further lowering of the vessel caused diminution of the tetanus, and finally its disappearance when the fluid was no longer above the crushed point. I could repeat this observation several times with the same preparation.

In by far the greater number of trials this experiment did not indeed give such evident results; at the moment that the nerve current is closed through the fluid a clonic agitation of the preparation occurs which soon disappears, or else the experiment is successful at the first trial only, or not at all. But in such cases even one may still get a reaction if the fluid is raised as rapidly as possible; a closure contraction then follows, as is generally the rule whenever the nerve-current of a moderately excitable preparation is suddenly closed externally.

According to previous observers[1], a reaction of the nerve-muscle preparation cannot be obtained if the transverse section is connected with a point of the longitudinal surface as near to it as possible. I have repeatedly succeeded in obtaining contraction under these circumstances, because I used preparations which were disposed to fall into tetanic excitation. If I made the experiment as soon as the preparation entirely ceased to contract in consequence of the freshly made section, and taking care to avoid any wetting of the nerve, the making contact between transverse and longitudinal sections gave me strong clonic agitation of particular groups of muscles. Moreover, I can point to instances in which there occurred strong closure contraction followed by clonic agitation, provided I had been able to establish contact with sufficient rapidity,—rather a difficult matter here.

The same holds good for an experiment which was made by Galvani, and which du Bois-Reymond designated as the fundamental experiment in the electro-physics of nerve, although he was not very successful in its repetition. 'Galvani arranged the nerve of a galvanoscopic leg as an open loop, and allowed the nerve of a second and otherwise completely isolated leg to fall upon the first nerve in such a way that the transverse section of the first nerve constituted one of the two points of contact. In favourable cases both legs contracted[2].' In speaking of the excitation of muscle

[1] See du Bois-Reymond, Unters. über thier. Elektr. ii. p. 272, and Kühne, *loc. cit.*

[2] Du Bois-Reymond, Unters. über thier. Elektr. i. p. 273.

by its own current, I have already mentioned that if the transversely cut ends of two Sartorius muscles are allowed to fall one upon the other with sufficient rapidity, and in such a way that the transverse sections are in the same plane, so constituting a single transverse section of both muscles, no contraction ever follows, whereas there may be a strong contraction of both muscles if one end of muscle falls upon the other so that the one is a prolongation of the other, but with the two ends overlapping. Now in the first case the two muscle-currents are opposed, and compensate each other; in the second, they have the same direction in the circuit, formed by the two ends of the muscles. Making use of this artifice, Kühne[1] has in fact obtained contractions with the nerve-current as well. I have likewise arranged the experiment on this plan, and found that it succeeds with certainty on sufficiently excitable frogs, provided only care be taken that the two ends of nerve have not too much fluid adhering to them. As soon as they were let fall one upon the other, the two legs contracted vigorously, and sometimes even passed into a prolonged clonic excitation. But if I dropped one nerve on the other so that the two transverse sections were in one plane, neither contraction nor tetanus occurred.

If the sciatic plexus of a cooled frog has been divided close to the vertebræ, or the nerves ligatured at that point, and then cut through above it, and if the cut bundle of nerves is raised, firstly by means of a fine glass rod, secondly by means of the thread, during the tetanus or clonus of the leg consequent on section of the nerves, it is frequently observed that the intensity of the tetanus or the form of the clonus is at once altered; if then the nerve is put back into its moist and conducting bed, the original type of contraction forthwith returns. One may repeat this with success several times. If the contractions of the leg are allowed to come to an end while the plexus is kept raised, and if the plexus is then replaced upon the ileo-coccygeal muscle, the contractions frequently reappear, although generally to a much less degree. This only occurs provided the ileo-coccygeal muscle has not been injured in the course of preparation. The cause of these phenomena (when muscle-currents do not play a part in them) is to be found simply in this, that when the plexus lies on the posterior wall of the pelvis, the nerve-current is closed externally to the nerve, whereas this is not the case when the plexus is raised.

[1] *Loc. cit.* p. 92.

The fact that sufficiently excitable nerves fall into persistent excitation if an external closure of low resistance is offered to their proper current, suggests that the above-described tetanic excitation which supervenes in cooled frogs after section of the sciatic nerve or plexus, is also simply due to the current which arises in consequence of the section. It must be remembered that this current exists in every single fibre, and that the sheath of each fibre, the fluid present between the fibres, as well as the common sheath of all the fibres, provide channels for external closure to each individual current. Consequently so soon as the nerve-current is produced by the transverse section, all the fibres fall under the influence of the nerve-current, the direction of which in the fibre is descending, and must excite it at the points of exit. Just as a weak battery-current excites tetanically any very excitable nerve, so, in the same way apparently must the proper current of nerve produce its excitation; and just as the lasting action of a current led in artificially is a gradually diminishing one, so the excitatory action of the nerve-current on the fibres of the nerve must be of limited duration. *Apparently, therefore, there is nothing opposed to the assumption that the more or less prolonged tetanic or clonic excitation of the muscles of cooled frogs consequent upon section of their nerves, is due to the nerve-current which results from section.*

That with this cause other causes participate, as regards the results of nerve section, is not, however, excluded by the above assumption. Just as any living substance can adapt itself to any persistent stimulus, so the nervous substance also adapts itself to a weak persistent current, whether this be an artificially applied one, or its own proper current. Provisionally one might, in accordance with custom, speak of this as 'fatigue.' In consequence of this adaptation or fatigue, the closure tetanus, or, in our case, the tetanus after nerve section comes to an end. A new external closure of the nerve-current effects, however, a sudden redistribution of current in the nerve, and therewith a renewed excitation.

Since other mechanical, thermic, and chemical agents act just like section in giving rise to the development of current in the nerve, there are many considerations regarding the mode of action of these stimuli and regarding the nature of nerve excitation which are suggested by these phenomena. I will not, however, yield to the temptation to enter upon theoretical considerations, just

as I refrained from doing concerning the excitation of muscle, and will confine myself to the suggestion which has just been made.

Excitation of the transverse section of a nerve by fluids.

Just as a muscle contracts so soon as its transverse section comes in contact with a conducting fluid, so does the nerve of a sufficiently excitable nerve-muscle preparation contract when the end of its nerve is dipped into a conducting fluid; and the contraction is apparently simultaneous with the contact. One is inclined to regard this contraction as caused merely by the sudden external closure of the nerve-current, and in harmony with this view is the fact that badly conducting fluids, such as alcohol, solution of corrosive sublimate, &c., do not give rise to the contraction at the moment of contact. But the assumption of a simultaneous chemical excitation of the nerve substance that has been laid bare by the incision, and is still perhaps, to some extent, excitable, cannot, in this case, be excluded in so easy and convincing a fashion as in the corresponding experiment on muscle.

As is well-known, Eckhard[1], who was the first to carry out systematic experiments relating to the excitation by fluids of the transverse section of nerves, considers this excitation to be exclusively chemical. He obtained no action by dipping the nerve into water, bisulphide of carbon, solutions of metallic salts (with the exception of nitrate of silver), organic acids such as gallic acid, and volatile oils.

The fluids which Eckhard found efficacious produced effects of two kinds. The first kind of action showed itself in a contraction at the instant of contact, the second followed if the nerve were dipped deeper, and consisted of contractions which began sooner or later after immersion, spread over a greater or smaller number of muscular fasciculi successively, and lasted for a very variable time, according to the agent employed, &c.

According to Eckhard the first contraction may be avoided if, instead of cutting the nerve, one ties it and immerses the tied end. With solutions of the fixed alcalies, provided they were not too weak, Eckhard obtained regularly both the contraction immediately following contact of the transverse section, and the subsequent contractions; mineral acids gave the second kind of contractions, and only very rarely the first. All the other fluids which Eckhard

[1] Die chemische Reizung der motorischen Froschnerven. Zeitschr. f. rat. Medic. Neue Folge, i. p. 302, 1851.

used with success—solutions of the haloid and neutral salts of the alcalies and alcaline earths, alcohol, ether, anhydrous acetic acid, saturated solutions of tartaric acid and of sugar—gave only the second kind of contractions.

From all these facts it appears to me that Eckhard worked with much less excitable preparations than I did. Although it was not my intention to make a special study of the excitatory action of fluids on the transverse sections of nerve, I incidentally made experiments of this nature with various fluids. And I found not only that concentrated solutions of sulphate of copper and sulphate of zinc (which, according to Eckhard, produce no effect) do produce effects in so far as they give contractions at the moment of their contact with the transverse section, but also that the same effect is obtained by the use of a concentrated solution of sodium chloride, and of 0·6 % solution of the same, fluids which, according to Eckhard, only give the second kind of contractions. Sulphuric acid, of a strength of 10 %, gave me the same result. Like Eckhard, I found the fixed alcalies especially active.

A small drop placed on a glass slip suffices for the production of the contraction by contact with sodium chloride, caustic potash, sodium carbonate, sulphuric acid, sulphate of zinc or of copper. I have seen solutions of sodium chloride, or of caustic potash, produce the effect when I had used for the purpose a tiny drop, sufficient to moisten the transverse section only, or at most the very border of the longitudinal surface in addition. I have not used such small drops of other fluids.

Now, although on account of what has been said above concerning the effect of external closure of the nerve-current, I cannot doubt that it plays an important part in the contractions occurring at the moment of contact, I am not in a position to be able to exclude the possible conjoint action of chemical stimulation. It surprised me that fluids differing but slightly in conductivity appeared nevertheless to behave quite differently as to the certainty with which they provoke contraction by their application to the transverse section. The great activity of the fixed alcalies may perhaps be explained by this, that the nerve is more rapidly and easily moistened by them than by other fluids, so that a more rapid electrical change is produced in the nerve. But I must leave it unsettled whether this is the reason of their apparently greater efficacy.

There are two circumstances which notably increase the difficulty

of this investigation. In the first place the specifically lighter nerve frequently fails to sink into a fluid which is of greater density than it, and rests on the surface, so that the external closure of the nerve-current is relatively slowly and incompletely established. In the second place one rarely succeeds in again obtaining the contraction by a renewed contact of the same transverse section with a fluid. I have already mentioned above, that the clinging of fluid to a nerve, and the permanent derivation thereby established, cause still more interference in this case than in that of muscle. Eckhard says indeed (*loc. cit.* p. 318), 'that one never succeeds in eliciting repeated contractions by repeated immersion of the surface of section.' I have, however, succeeded several times in obtaining repeated contractions at the instant of immersion, still this was, on the whole, a rarity. As regards the question merely of demonstrating the action of the nerve-current, it would be of little interest to prosecute these experiments; but in relation to the question of chemical excitation it would be of considerable importance if one could distinguish between the electrical and the possibly coincident chemical stimulation at immersion of the transverse section. If anyone chose to maintain that the so-called chemical excitation is only electrical, and is efficient only in so far as it gives rise to current as well as chemical alteration, this could hardly be disproved in the present state of our knowledge.

The same difficulty which is presented by the contraction occurring at contact of the transverse section, repeats itself as regards the subsequent irregular contractions. For when the nerve-current was externally closed by other means we saw the same thing occur, provided the preparations were very excitable. The question must eventually arise as regards such preparations, what is to be regarded as due to the electrical, and what to the chemical excitation, when a long-enduring agitation results from dipping the nerve into a fluid. If it is possible (as in the experiment with normal saline, described at p. 139) to repeat, with always the same effect, the immersion of an electromotive portion of nerve, it is allowable to exclude any chemical action. But if the experiment succeeds only at the first immersion, its interpretation remains very doubtful. The experiments of Eckhard, which cannot but awaken the keen interest of any one who repeats them, and especially the remarkable action of the fixed alcalies, were well worth a renewed methodical investigation.

2. On true secondary contraction and secondary tetanus derived from nerve.

On the behaviour of nerve when it is excited by induction currents in the vicinity of a transverse section.

Before passing to the subject-matter proper of this section, I will refer to the peculiar behaviour which a nerve manifests when it is excited by induction currents in the neighbourhood of its transverse section, for this is of importance to what has to follow.

If to a freshly cut or tied nerve the electrodes of the secondary coil are applied, separated from each other by a distance of only two to three mm., so that one electrode is at the point of section or of ligature, the very weakest currents give strong contractions if the direction of the break-currents is abterminal in the nerve. With an atterminal direction of these currents the contraction is much weaker, or absent, in spite of unaltered position of the electrodes and unaltered current strength. If, the direction of the break-currents being abterminal, the electrodes are pushed further and further from the transverse section, the effects diminish rapidly to zero. If, on the other hand, the direction of the break-currents is atterminal, the effect rapidly increases as the electrodes are moved away from the transverse section, soon reaching a maximum, and finally diminishing and disappearing as the electrodes are moved still further away. All this naturally presupposes that one is working with minimal current strengths and freshly-made transverse sections.

The rule here given is however liable to exceptions. If there are points of section of branches in the vicinity of the transverse section, if the latter is not quite fresh, if the nerve has been injured in its course, or sometimes from other undemonstrable causes, departures from the rule may present themselves. I am here concerned only with the rule itself which anyone will easily find to hold good. From it one may generally determine, with complete certainty, the direction of the break-current in given cases.

This behaviour of the nerves is especially valuable in all those cases in which it is desired without further trouble to exclude unipolar effects. For on the one hand the low intensity of the currents used makes these effects very improbable, and on the other they ought to persist or indeed become stronger as the electrodes are moved away from the transverse section, and consequently towards where the nerve produces its action; whereas, indeed, under the circumstances in question, the opposite is the case.

It was during experiments on excitation of the central end of the vagus that I was first struck by the fact that it is necessary, in order to obtain an effect, to bring the secondary much closer to the primary coil when the break-induction shocks are atterminal than when they are abterminal. Since then I have noted and found this confirmed in the excitation of various nerves of warm-blooded animals. Nerves of frogs behave similarly. But in these, unless it is specially desired to investigate excitability in the neighbourhood of the transverse section, it is seldom necessary to place an electrode at or near a transverse section or ligatured point, whereas in warm-blooded animals, owing to shortness of the end of nerve, this frequently has to be done. In such cases, it is easy to convince oneself of the great difference in the effect when the electrodes are shifted, or when the current is reversed. Nor does the Helmholtz modification entirely abolish the difference.

Although the peculiar conditions of excitability of nerve in the neighbourhood of its transverse section have been frequently investigated since Heidenhain called attention to them, I think that the facts which are here mentioned, and which are, in many respects, important, have not been sufficiently regarded. To experimenters familiar with the department of nerve physiology, this is perhaps no novel statement.

On the excitation of nerve consequent upon the negative variation of the current of another nerve lying upon it.

If no one has yet succeeded in obtaining true secondary contraction from nerve, this want of success must be attributed to the fact that all the attainable conditions which favour it have not been utilised. When I took advantage of these, I succeeded in eliciting from nerve true secondary contraction and secondary tetanus which were as strong and as lasting as if the nerve of the secondary preparation were itself directly excited electrically.

In designating these as 'true' secondary effects in contradistinction from the secondary effects discovered by du Bois-Reymond, and caused by the electrotonic currents of the primary nerve, I am justified on the one hand, by the convenience of the term, on the other, by the consideration that the secondary effects to be presently described are truly analogous with the secondary contraction from muscle. This, as the longest known kind of secondary contraction, deserves to be regarded as the prototype of such actions.

The great excitability exhibited by the nerves of cooled frogs in the vicinity of a freshly-made transverse section, led me to choose the central end of such a nerve as the point of excitation of the secondary preparation. I laid bare the two sciatic nerves from the spinal column to near the knee, and used one of these nerves, divided at both ends, as the primary, the other still connected with the leg as the secondary preparation. The peripheral end of the primary nerve was placed upon the central end of the secondary, so that both nerves lay close together for a space of five or six millimeters, and with their transverse sections in one plane. With this arrangement, the current of one nerve, so to speak, compensates that of the other. Granting now that in consequence of a momentary excitation of the primary nerve, the current suddenly vanishes in its peripheral end (negative variation down to zero), then the compensation of the current of the overlying secondary nerve is thereby suddenly removed; at this moment the end of the primary nerve being suddenly deprived of current acts merely as an external closure to the current of the secondary nerve, and the latter, by this sudden derivation of its proper current, must suffer a weak excitation. But if, as Bernstein once supposed[1], the current of the excited nerve actually alters its direction, this current will, after its reversal, act upon the secondary nerve as a weak descending current, which is added to the proper current in that nerve at the moment that this is closed externally.

Before tetanising the central end of the primary nerve by means of weak induction currents, I provided its peripheral end, and at the same time the central end of the adjacent secondary nerve, with a new transverse section common to both, by a single stroke of the scissors. *I thus actually succeeded in provoking weak tetanic agitation of the secondary preparation at each tetanisation of the primary nerve.* Of escape of current or of unipolar action there could be no question, seeing that the exciting currents acting upon the central end of the primary nerve were so weak as to be only just efficacious when the electrodes were placed near the transverse section, and that all secondary action was absent when I moved the electrodes to a part of the primary nerve nearer to the secondary preparation.

In so far as one may regard as excluded any excitation of the secondary nerve by electrotonic currents—the distance from the point of excitation to that of contact with the secondary nerve being

[1] Untersuchungen über den Erregungsvorgang im Nerven und Muskelsystem, § 9, 1871.

equal to almost the entire length of a sciatic nerve, and the distance of secondary from primary coil being as much as 40 cm. (1 Dan. 6000 turns of sec. coil.)—*it was settled by this experiment that true secondary action is possible from nerve to nerve.* If I placed the two nerves together, so that one was a prolongation of the other, with their two ends however in contact for 5 or 6 mm., all secondary action was absent, as indeed was to be expected on theoretical grounds.

But still the above-described weak and exceptional results were not sufficient to satisfy me. I saw that everything depended upon the most intimate contact between the two ends of nerve, and that if it were at all incomplete, or if the nerves had but a very little lymph or salt solution adhering to them, the result was interfered with. And so I came to think that it is very unpractical to take great trouble in applying two nerves to each other, instead of using a preparation in which the two bundles of nerve-fibres, which are to serve as primary and secondary respectively, lie together naturally in the same sheath.

I decapitated a cooled frog, removed the upper extremities and intestines, laid bare the sciatic nerve above the knee, ligatured with the same thread its two branches, divided them below the ligature, prepared the nerve up to near the point of origin of the branches to the muscles of the thigh, divided the sciatic plexus, waited until the consequent disturbance had subsided, and then, when all the muscles were quiescent, excited the end of the nerve at the knee with weak induction currents. *The muscles, the nerves of which were still in connection with the plexus, entered forthwith into strong secondary tetanus,* just as if I had excited these nerves directly.

Often as I have since repeated this experiment it has never failed, provided only that the preparation was sufficiently excitable to give, in addition to the single contraction, a weak and fugitive muscular disturbance in the thigh when the sciatic plexus was divided. But I have also made the experiment with almost constantly successful result, on cooled frogs—land frogs in particular—which did not give the tetanic agitation after nerve section, if only I excited the peripheral end of the sciatic very shortly after section. In those cases, it is true, a strong secondary tetanus was not reached; there was for the most part only a tetanic or clonic agitation of the muscles, just as may be seen with nerve-muscle preparations, the nerves of which are excited with excessively weak, that is to say barely efficacious, induction currents.

In this experiment the secondary tetanus appears not merely in the muscles which are innervated from the femoral branches of the sciatic, but also in the muscles which are supplied by the crural nerve, which arises from the plexus itself. If the femoral branch is divided, and the sciatic isolated up to the origin of the crural, excitation of the end of the sciatic at the knee gives rise to secondary tetanus at the muscles innervated by the crural. I have also isolated the sciatic nerve in its whole course down to the branch which goes to the semimembranosus and rectus internus, then divided the sciatic above the knee and removed all the rest of the limb with the exception of the above-named muscles, and finally separated the plexus from the spinal column, so that the whole nerve, with these two muscles in connection with it, was completely isolated. These muscles became secondarily tetanised when I applied weak induction currents to the peripheral end of the nerve.

If instead of dividing the plexus I divided the spinal column with its nerves between the seventh and eighth, or between the eighth and ninth vertebræ, I only exceptionally obtained secondary tetanus. But on the other hand, I have recorded one case in which the division had been made between the sixth and seventh vertebræ, and in which excitation of the peripheral end of the sciatic gave rise to very strong secondary tetanus of the muscles of the thigh and of the trunk on the corresponding side of the body. The mode of this tetanus did not allow of its being considered as reflex, although the incision had reached the lowest part of the spinal cord—which moreover, according to Engelhard[1], is incapable of giving reflex movements.

If after division of the plexus I severed and excited one only of the two branches into which the sciatic divides above the knee, I obtained often, but not always, secondary effects which manifested themselves, partly in the muscles of the thigh, partly in the leg muscles supplied by the other of the two branches. But still this secondary action rarely reached to a steady enduring tetanus, and generally went no further than a tetanic agitation. Once indeed I obtained secondary action by tetanising the sural nerve which I had divided at the ankle joint and prepared up to the knee: the toes spread out vigorously, and the gastrocnemius fell into clonic contractions. Unfortunately the muscles of the thigh were not observed, and I did not succeed in repeating the experiment

[1] Müller's Arch. f. Anat. u. Physiol. Jahrg. 1841, p. 208.

with any satisfactory result. I may mention finally that I have repeatedly obtained secondary tetanus of the muscles supplied by the axillary plexus, by peripheral excitation of the ulnar nerve prepared up to the axilla and divided above the elbow, the axillary plexus having been previously divided.

It can not be supposed that the above-described secondary effects can be attributed to escape of current or to unipolar excitation. The electrodes—fine platinum wires, 2 or at most 3 mm. apart—were placed quite close to the transverse section, so that the break induction currents were ascending (abterminal) in the nerve, and the induction coils used with one Daniell were separated by a distance of from 50 to 40 cm. or at most 30 cm. for comparatively less excitable preparations. Such weak induction currents, although acting energetically close to the transverse section, generally lost all effect as soon as I moved the electrodes further away from the transverse section towards the muscles. Whenever this was not the case I did not regard the experiment as completely trustworthy. If I made the induction currents descending (atterminal) in the nerve, I obtained no effect with currents which had acted energetically in the opposite direction, so long as the electrodes were very near the transverse section. Effects were produced however, either with the same or with a somewhat increased current strength, as soon as I moved up the electrodes from the end of the nerve at the knee; generally disappearing again if I brought the electrodes still nearer to the muscles. There were however exceptions to this. These facts are sufficient to make the above-named objection inadmissible. But as regards the possibility that my experiments have in them nothing but the paradoxical contraction described by du Bois-Reymond, I shall presently discuss this matter for the satisfaction of those who may still have doubts.

I have not confined myself to obtaining secondary tetanus by tetanising the primary nerve with induction currents, but I have also used with the same result weak battery-currents, rendered tetanising by means of a rotating commutator.

Further, I have obtained strong secondary single contractions in great number by means of single induction shocks and by closure of weak battery-currents. What weak currents suffice for this purpose is shown, for instance, by an experiment in which, with one Daniell and only 4·5 cm. of the double wire of du Bois-Reymond's rheochord as resistance, I obtained a strong secondary contraction at each closure, when I made this weak current

ascending (abterminal) in the end of a sciatic nerve which I had divided above the knee.

Just as it is possible to obtain secondary contraction or secondary tetanus from any muscle which is set in action by excitation of its nerve, when the nerve of the secondary is laid upon the muscle of the primary preparation, so it is possible to obtain similar effects in muscles in which contraction is produced by secondary action derived from nerve. If I caused secondary contraction of the thigh muscles as above described by the application of weak induction currents to the extremity of the sciatic nerve at the knee, then a second nerve-muscle preparation with its nerve lying upon the thigh-muscles of the first frog gave what I may call 'tertiary' contraction, and it passed into strong or 'tertiary' tetanus even when the currents applied to the first nerve were only just sufficient to tetanise it.

I have already pointed out above that the secondary contractions from nerve are most easily obtained just after the plexus has been divided. It follows that with the repetition of the experiment upon otherwise quite unaltered preparations, the secondary action diminishes more and more and finally ceases. This is not at all due to fatigue alone, but chiefly to the decline of the nerve excitability which had been previously enhanced owing to the section. For even if one waits a little after division of the nerve without subjecting it to excitation, and then excites, the secondary action is weak or absent. With comparatively sluggish preparations a delay of a few seconds is usually sufficient for this to be shown, but with good preparations several minutes on an average are required. But if a new transverse section is now made at the plexus, or if it is ligatured or crushed below the point where it was first divided, excitation of the peripheral end of the nerve, when the muscles have come to rest, gives, with good preparations, renewed and strong secondary effects. In this way, and without altering the seat of peripheral excitation, I have reproduced the secondary effects with the same preparation after they had vanished, as many as six times. It however often happens with less excitable preparations, that a secondary effect is obtained only after the first severance of the plexus. This rapid disappearance of the heightened excitability consequent upon section which is necessary to the success of the experiment, is the real reason why these have escaped the attention of previous investigators and especially of du Bois-Reymond, who must otherwise certainly have met with them in the course of his experiments on paradoxical contraction.

If the sciatic nerve is cut a few millimeters above the origin of its femoral branches, excitation of the nerve at the knee with the above-mentioned weak currents usually gives a very weak secondary effect or none at all. A similar result follows if the sciatic is cut above its division into tibial and peroneal nerves, and either of these is divided as far down as possible and excited at its peripheral end. Perhaps this is due to the fact that at these points the fibres of the branches in question have already separated from the remaining fibres so as to be gathered together in separate bundles, although they are contained in the same common sheath with these remaining fibres. In the plexus itself the fibres which are submitted to direct excitation are apparently mingled with those which are to be indirectly excited, a disposition which must be very favourable to secondary excitation. But besides this it is possible that a greater excitability of the fibres within the plexus is to be taken into account. I have sought in vain to obtain secondary contraction by dipping into hot water the foot of the leg of which the plexus had been just previously divided ; and I have in vain suddenly frozen, or touched with a hot glass rod, the peripheral end of a sciatic nerve which had been laid bare and cut above the knee ; secondary contraction was never obtained. But with crushing of the nerve I have seen a very weak and partial contraction of a thigh-muscle twice and three times in succession at each crushing, in two cases out of three preparations. I should not like however to lay much stress upon this, seeing the large number of unsuccessful experiments I have made.

These negative results need not be surprising if one bears in mind how difficult it is to produce a strong negative variation of the nerve-current by non-electrical excitation, and how much more certainly the secondary contraction derived from muscle itself is produced, when the nerve of the primary preparation is excited electrically, than when other stimuli are employed. Indeed a steady and enduring tetanus can be obtained only by electrical excitation of the primary nerve.

Distinction between the true secondary contraction and the paradoxical contraction of du Bois-Reymond.

As is well known, du Bois-Reymond observed that when a sciatic nerve which had been severed from the spinal cord was excited electrically, muscles supplied by branches which left the nerve above the point of excitation, contracted, and that he called

these contractions 'paradoxical.' He observed contraction of the muscles supplied by the peroneal nerve when the tibial nerve was excited, and *vice versa*, and with excitation of the sciatic below the origin of its femoral branches he saw contraction of the muscles supplied by these nerves. He showed that the contractions in question are caused by electrotonic currents which pass from excited to adjacent fibres. And in point of fact the conditions of his experiments were such that there can be no doubt concerning the correctness of this explanation. For he sent the whole current of a Grove's cell through the nerve by means of platinum electrodes, and observed that the paradoxical contraction appeared with greater certainty and strength as the electrodes were brought closer to the point where the indirectly excited nerve branched off. According to a figure which he gives of the arrangement of an experiment, the point where the nerve branches and the nearest electrode are distant from each other by not more than about 7 mm.

I have experimented under quite different conditions. In using the battery-current, for instance, the weak currents which are obtained with one Daniell and only 1 to 2 mm. of the du Bois-Reymond rheochord consisting in a double wire of platinum, were sufficient. The platinum electrodes were distant from each other about 2 mm., and between the femoral branches the muscles of which were excited to secondary action and the nearest electrode, there was a length of nerve of at least 30 mm. If I used unpolarisable electrodes, no more than 25 mm. of the rheochord wire were required to give the same result. With induction currents, using only 1 Dan., it was often sufficient to place the secondary coil at a distance of 50 cm. in order to obtain strong secondary effects in the thigh when the sciatic nerve was tetanised at the knee. I have also repeatedly divided the femoral branches, so that none remained attached to the sciatic nerve between the electrodes and the origin of the crural nerve from the plexus 40 to 42 mm. higher up. Under these circumstances the muscles supplied by the crural nerve were excited to strong secondary tetanus when I tetanised the sciatic at the knee with the coil standing at a distance of about 40 cm. Whereas du Bois-Reymond obtained stronger secondary effects the nearer he moved the electrodes to the branch, I obtained progressively weaker effects which soon disappeared, if I moved the electrodes further from the section, i.e. nearer to the branches that were to be secondarily excited, especially with ascending (abterminal) currents,

This indeed only held good with very weak currents. If I made use of considerably stronger currents, I could then obtain effects by placing the electrodes at various parts of the nerve, and if I placed them very near the origin of the femoral branches, the secondary action was sometimes suddenly and strongly increased owing to the presence of electrotonic currents. From all this it appears that the effects observed by me are above all a function of the excitability of the part of the nerve to which the electrical stimulus is applied, while those which du Bois-Reymond has recorded are rather a function of current-strength and of the distance of the point of excitation from the secondarily excited nerve.

In point of fact these experiments of mine and those of du Bois-Reymond, in spite of their superficial analogy, are concerned with two fundamentally distinct classes of phenomena. The true secondary contraction is dependent upon the excitation propagated to the central end of the divided nerve and consequent variation of the nerve-current. If, instead of secondarily excited fibres in contiguity with the directly excited fibres in the central end of the nerve, we imagine a muscle in natural connection with the directly excited fibres, we may lay down the following rule as regards the result of our experiments: *If this muscle contracts strongly, the muscle of a secondarily excited nerve will also contract.* This rule signifies, then, that the true secondary contraction must follow the law of contraction, just as would be the case for a muscle in connection with the central end of the primarly excited nerve. Apparent departures from this rule are simply due to the fact that the excitability of the secondary nerve does not remain so constant as that of a muscle, but rapidly diminishes after the cross section is made.

The paradoxical contractions of du Bois-Reymond follow quite another rule. An example will show this best. The sciatic nerve is divided above the knee, isolated up to its femoral branches and placed upon unpolarisable electrodes, so that the interpolar region is not more than a few millimeters long, and the transverse section is but a few millimeters distant from the nearest electrode. The rheochord is in conjunction with 3 or 4 Daniells, and one pole of the battery is joined to the removable binding-screw of the rheochord, so that a weak branch current or the total battery current can be alternately sent through the nerve. All the plugs are put in, the slider of the rheochord is placed at zero, and the direction of current is such that the derived current is descending (atterminal) in the sciatic nerve. The sciatic plexus is now divided, and

by moving the slider the derived current is increased until there is a secondary contraction at closure. This requires, according to the excitability of the preparation, either an extremely small distance of the rheochord slider, or with comparatively poor preparations, a distance of at most a few centimeters. At opening of this weak current there is no secondary contraction. The above-mentioned rheochord binding-screw is now withdrawn, so that the entire current of the battery is sent through the nerve: *there is no longer any secondary contraction at closure,* because the electrotonic alteration of the nerve at the anode blocks the excitation proceeding from the kathode. Opening of this current gives strong secondary contraction with sufficiently excitable preparations; with such as are less so, the contraction fails in this case also. If now the weak derived current is restored, its closure gives a contraction, and its opening has no effect, whereas renewed establishment of the strong current has no effect at closure, but gives an opening contraction. In this manner the alternate excitation with weak and strong currents can be carried on so long as the preparation remains excitable; the weak current giving only a make-contraction, the strong current only a break-contraction, or, if the excitability is already depressed, no contraction at all, at a time when the weak current can still give rise to secondary contraction at make.

But if in the case of the strong current the electrodes are brought so near to the femoral branches of the nerve that electrotonic currents act upon the fibres of these branches which are contiguous with excited fibres, the paradoxical contractions of du Bois-Reymond are produced, *and now the strong descending (atterminal) battery-current gives a make-contraction; but the weak current applied to the same point generally gives no contraction,* for its strength was such that it was only just adequate to evoke secondary contraction when it was applied to the lower transverse section, i. e. to the most excitable part of the nerve.

It appears thus, that, as regards the true secondary contraction, everything depends upon whether a sufficiently strong excitation wave is propagated to the central end of the primary nerve-fibres, there to give rise to excitation of adjacent fibres by means of the negative variation of the nerve-current. Very weak currents are sufficient for this, provided they are applied to the most excitable portion of the primary nerve. The distance between the excited point and the origin of the fibres to be excited secondarily is in the main indifferent. But in the case of du Bois-Reymond's secondary

contraction, the problem is to excite by means of sufficiently strong electrotonic currents in directly excited fibres, other fibres adjacent to these, and to excite them near the point where they part company from the directly excited fibres. To this end are required strong currents and a small distance from the excited point to the point of branching.

If the transverse section of a nerve trunk, of which one branch is to act as the primary and the other as the secondary nerve, is in the vicinity of the point of branching, the increased excitability of the secondary nerve fibres in the neighbourhood of the transverse section may favour secondary excitation by means of the electrotonic currents. As a matter of fact du Bois-Reymond has already found that when the peroneal or tibial nerve is excited, a fresh transverse section of the sciatic favours the appearance of the paradoxical contraction in the muscles supplied by the branch which is not directly excited. And in this case the presence or absence of a paradoxical contraction at make or at break is notably affected by the direction of the electrotonising current, since the part of the secondary nerve which is to be excited by the electrotonic currents lies very close to the transverse section of that nerve.

It is easy to understand further, that when strong currents are applied near the origin of a nerve which is to be excited indirectly, the effects of the electrotonic currents may combine with the effect of the negative variation, if the preparation is excitable enough, and especially if the transverse section is still fresh. It is my intention to consider these complex cases after discussing more completely the paradoxical contraction of du Bois-Reymond. If the above directions are observed, there will be no danger of the admixture of electrotonic action. The current ought to be so weak that when it is ascending (abterminal) it acts only when quite close to the transverse section, or at any rate much more strongly here than at any other part of the nerve. With descending (atterminal) currents even when of excessive strength, the true secondary contraction may be distinguished from the other by the fact that the former disappears when the current is made so strong that the nerve is blocked in the region of the anode (3 to 4 Daniells), whereas du Bois-Reymond's secondary contraction increases with increasing current-strength.

PART II.

RESEARCHES

RELATING TO

SECONDARY ELECTROMOTIVE PHENOMENA.

VI.

ON SECONDARY ELECTROMOTIVE PHENOMENA IN MUSCLES, NERVES, AND ELECTRICAL ORGANS.

By E. DU BOIS-REYMOND.

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VI.

1. Introduction.

I THINK it is now time to break the silence which I have hitherto maintained regarding certain experiments on animal electricity with which I have been occupied for nearly forty years, and to which I attach great importance. I should have been glad to complete this research as far as I was able before publishing the results, but recently electro-physiologists have approached from several sides the province in which I was for so long the only worker, so that by holding back any longer I incur the danger of forfeiting my share of the fruit of a work, respecting which I have more than quadrupled the *nonum prematur in annum*. I shall therefore now state the chief views at which I have arrived. In future papers I shall develop more fully what I have said here.

Long ago I divided the electromotive phenomena of muscle and nerve into three classes [1]. The first are perceptible without the co-operation of an extraneous current in a condition of rest or action. To these belongs the current of muscle or nerve at rest as well as its negative variation, the case in which the latter is induced electrically being included in so far as the tetanising current is replaceable by any other excitation. If we wish to extend the classification to electrical organs, we must also include in the same class the weak electromotive effects observed in them when at rest, which I call 'the organ current [2],' and the shock of the organ in whatever way induced.

In the second class I placed the extra polar electrotonic currents which appear in nerves during the continuance of an extraneous current and to which there exists nothing analogous in muscle or in electrical organs [3].

[1] Untersuchungen über thierische Elektricität, vol. ii. part ii. p. 377.

[2] Dr. Carl Sachs' Untersuchungen am Zitteraal, Gymnotus electricus, nach seinem Tode bearbeitet von E. du Bois-Reymond, Leipzig, 1881, p. 171 ff.

[3] Eckhard experimented on the organ of the 'Torpedo,' Sachs on that of the electrical eel, in order to obtain electromotive action of the electrical organs by a

To these two long known classes I added a third—that of secondary electromotive phenomena; by which term I understand those electromotive phenomena which an extraneous current produces in the portion of muscle it flows through, and which can generally only be observed owing to their lasting longer than the extraneous current. These are the facts, to a great extent new, about which I intend to treat. As I shall presently mention, however, it will be found that a distinction can hardly be maintained between the two last classes.

Secondary electromotive phenomena appear for the most part as polarisation-currents. I prefer the former of these two expressions, which is quite applicable to the ordinary phenomena of polarisation, and could be used to designate the apparent polarisation of muscles and nerves, even though it should prove to be different from galvanic polarisation. I do not, however, insist pedantically on the name, but occasionally call the secondary current, generated by the secondary electromotive force, the polarisation-current, and also the after-current; while the primary current which induces it is styled the polarising current. I also find it sometimes convenient to speak of the body to be polarised as 'object of polarisation.' By negative I mean a polarisation-current in an opposite direction to the primary current, and by positive one in the same direction.

2. Historical.

At the commencement of my researches in science I encountered a phenomenon which belongs to this subject. Peltier described in 1836 a negative polarisation in a frog's limb through which a current was passing, which he compared to the polarisation of the metals in Ritter's secondary battery. According to him the seat of the polarisation was in the part of the limb immersed in the

persistent passage of the current; Eckhard unsuccessfully, Sachs with doubtful results (Untersuchungen am Zitteraal u. s. w., p. 188 *et seq.*). Even if these experiments had succeeded one could not speak of electrotonus of electrical organs. In muscles Hermann thinks he has now found a trace of that electrotonus current which formerly neither he nor I could prove, and which his theory so urgently required (Handbuch der Physiologie, vol. ii. Leipzig, 1878, p. 168)—Die Ergebnisse neuerer Untersuchungen auf dem Gebiete der thierischen Elektricität. Separat-Abdruck aus der Vierteljahrschrift der naturforschenden Gesellschaft in Zürich, 1878, pp. 21, 22. He does not consider the possibility that the observed action may proceed from the intramuscular nerves. As early as in 1849 I warned against this fallacy (Untersuchungen, vol. ii. part i. p. 330).

water which conveyed the current. When he applied a galvanometer to the parts intermediate between the submerged ones, through which the current had passed, no action whatever was observed.

In consequence of this Peltier considered the cause of the polarisation to be the separation of hydrogen and oxygen in the submerged parts, which he assumed from the analogy of metallic electrodes, without however demonstrating anything of the sort [1].

Peltier's observation was the starting-point of my own work on this subject. On repeating his experiment with a solution of ordinary salt instead of water, I actually found the surface where the current entered the preparation giving an alkaline reaction, and where it emerged giving an acid reaction [2]. Though this appeared favourable to Peltier's explanation, yet, on the other hand, I found, in opposition to his assertion, that every part of the preparation through which the current had passed possessed, like a secondary battery, a negative electromotive action. A portion, then, of the negative polarisation possibly depends on the ions collected at the points where the current enters and leaves the preparation. The largest and by far the most important part has its seat in the interior of the tissues, no doubt principally in the muscles.

3. Preliminary Studies on the internal Polarisation of moist porous bodies.

I was thus led to conceive the idea of an internal polarisation of muscle. I soon, however, found other moist porous bodies susceptible of internal polarisation, and then I first traced the new phenomenon from a purely physical point of view through a long series of moist porous bodies. These were either of an inorganic or

[1] Untersuchungen über thierische Elektricität, vol. i. part i. p. 377; vol. ii. part ii. p. 378.

[2] Humphry Davy saw acid and alkali set free in muscular flesh, pieces of living plants, and even in the fingers to which distilled water had conducted the current. (Philosophical Transactions for the Year 1807, Pt. I. pp. 52, 53; cf. Simon in Gilbert's Annalen, 1801, vol. viii. p. 28; Ritter loc. cit., vol. ix. p. 329. I also saw acid and alkali set free in a water-pad covered with violet-blue litmus paper between saline pads. (Gesammelte Abhandlungen zur allgemeinen Muskel- und Nervenphysik, vol. i. Leipzig 1875, p. 11.) When I said here that this was contrary to Davy's statement that test-paper only changes colour at the metal electrodes through ions, the above experiments of Davy's were not before me.

an organic nature, and in the case of the latter either organised or not organised. In the latter case, again, they might be either dead like wood, or living like fresh tissue of plants[1]. It may be stated generally that every porous body which is not too bad a conductor and is soaked with an electrolyte which, in comparison with the porous body, does not conduct too well, is susceptible of negative internal polarisation; i. e. after the passage of the current each transverse section lying between two isoelectric surfaces has an electromotive action in a direction opposite to that of the polarising current. This can be explained by the supposition that the current divides itself between the soaking fluid and the porous framework, and that the latter becomes polarised just like a metallic septum by the ions set free on its surface. Each one of the innumerable minute septa has an electromotive action in a direction opposite to that through which the current passed. The partial currents thus generated take their way through two paths, one presented by the internally polarised body itself, the other by the galvanometer-circuit applied to the body. Their strength in the latter depends on the dimensions of the polarisation-object, on the position of the little septa in its interior, on the nature of the material composing the porous framework, and on the soaking fluid. The total current in the galvanometer-circuit results from the superposition of all the partial currents, whose strength is naturally an unknown and complicated function of the strength and duration of the polarising current, and the length of time since its opening. All that can be said is that it must increase with the increase of the two first variables up to a certain point, and must diminish with that of the third.

We have a clear example of internal polarisation in a cylinder of thoroughly burned wood-charcoal soaked with weak sulphuric acid, and through which a current is passed axially. As a material it conducts sufficiently well, so that a portion of the current finds its way through it notwithstanding the good derivation which the dilute acid affords. Each tract of the charcoal cylinder of equal length has an equally strong secondary electromotive action. The action of the whole cylinder equals the sum of all the individual tracts. Wood is also capable of strong internal polarisation. It is necessary, however, as the substance of the wood conducts badly,

[1] Untersuchungen über thierische Elektricität, vol. i. part i. p. 380. Gesammelte Abhandlungen, loc. cit. 13–28: 'Über innere Polarisation poröser, mit Elektrolyten getränkter Halbleiter' (August 4, 1856).

that the soaking fluid should not belong to the class of better conductors. Only a weak action is obtained with solution of common salt and of sulphate of copper. The best liquid to use is distilled water. I studied on prisms of wood the effect of the length and sectional size of bodies susceptible of internal polarisation, upon the strength of the polarisation-current under circumstances in other respects the same. In the first place, it is apparent that in internal polarisation it is not the strength but the density of the current which comes into consideration. In accordance herewith it became further apparent that the strength of the internal polarisation is a function of the resistance of the moist porous body, in so far as this resistance is determined by the dimensions. This function possesses a maximum, which, in a given circuit, the length of the internally polarisable body remaining constant while the transverse section increases, is arrived at the later, the more imperfectly the soaking fluid conducts [1].

4. Continuation of Preliminary Studies. On Polarisation at the surface of contact of dissimilar Electrolytes.

While studying internal polarisation I met with facts showing a second kind of polarisation in moist conductors, i.e. the polarisation at the surface of contact of dissimilar electrolytes. In contrast with internal polarisation it possesses the peculiarity that it can also be positive. If there is at the same time in the circuit an internally polarisable body, action in opposite directions (doppelsinnige Wirkung) is often obtained, i.e. a deflection first in one direction and then in the other [2]. If, for instance, a pad of blotting-paper soaked with water placed between two pads of the same sort soaked with a solution of common salt has a current passed through it, there follows on the opening of the polarising circuit and the closing of the galvanometer-circuit, first a negative preliminary deflection (Vorschlag), which is immediately followed by a positive deflection of longer duration. The preliminary negative deflection arises from internal polarisation of the water-pad, the positive from the sum of the positive polarisations at the contact of salt solution with water,

[1] Gesammelte Abhandlungen, vol. i. pp. 29-41: 'Über den Einfluss welchen die Dimensionen innerlich polarisirbarer Körper auf die Grösse der secundär Elektromotorischen Wirkung üben' (January 31, 1859).

[2] Op. cit. vol. ii. Leipzig, 1877, p. 407.

and water with salt solution. The internal polarisation in this case is stronger but more evanescent in character, the external weaker but more lasting, which explains the slight negative first deflection, followed by a principal deflection which is positive.

All the fresh animal tissues which I have examined behave between two saline pads like a water-pad. A piece of rib, costal cartilage, sinew, elastic tissue, frog's skin, human skin, pieces of lung, liver, spleen, rabbit's kidneys, and lastly, muscles and nerves—they all assume positive external polarisation which sums itself algebraically with internal negative polarisation. Under circumstances otherwise the same, the latter is more strongly developed the greater the length of the portion of tissue through which the current is passed [1]. If animal tissues are exposed to a current between the usual pads soaked with a solution of sulphate of zinc, and covered with a layer of clay, kneaded with a 'physiological' solution of common salt (i.e. 0·6 per cent.), the external polarisation is very little marked [2]. But it is advisable, in order to avoid errors in investigation of the internal polarisation of muscles and nerves, not to lead off the secondary electromotive polarisation current by means of the same pads, clay tips, &c. by which the primary current has been led through it, or at least not to lose sight of the fact that if this arrangement becomes necessary under certain circumstances, polarisation at the boundaries of the dissimilar electrolytes may come into play.

5. Further Continuation of Preliminary Studies. External and Internal Polarisation of moist porous bodies.

When I reached this point I thought I knew enough of what takes place during the passage of a current through a series of moist porous bodies, to enable me safely to continue my researches on the secondary electromotive phenomena of muscles and nerves. But I found myself greatly mistaken. After I had made numerous experiments of this kind I discovered a new source of error, by which my work up to this time was rendered, if not useless, at least inadequate. This was what I have called 'secondary resistance' of moist porous bodies, which I now made the subject of a long

[1] Op. cit. vol. i. pp. 1–12: 'Über Polarisation an der Grenze ungleichartiger Elektrolyte' (July 17, 1856).

[2] Op. cit. vol. ii. pp. 189 ff.

and wearisome course of experiments[1]. I understand by this a resistance which is created by the current itself; which on cessation of the current gradually decreases; and which on its reversal gradually disappears. The secondary resistance which is developed in coagulated albumen between zinc pads is capable of weakening the current from a Grove's battery of twenty elements, to such an extent, that only a tenth of the original strength remains. Consequently, the secondary resistance may greatly surpass the increase of conducting power consequent on the warming of a moist porous body by the passage of the current through it. Reversal of the current in moist porous bodies in which secondary resistance prevails, does not, like reversal in polarised conductors, give rise to a sudden positive increase in the strength of the current, but it presents the remarkable phenomenon of a gradual increase, which goes on for some minutes, until the current almost reaches its original height. From this point the decrease begins, to be again exchanged for slow increase if the current is once more reversed.

There are two kinds of secondary resistance, i.e. an external and an internal secondary resistance, corresponding to the external and internal polarisation of moist porous bodies. The seat of the first is the point where the current enters, and although much remains obscure, it may be explained by the cataphoric action of the current driving the fluid in the circuit onwards from the anode to the kathode. Where a zinc pad conducts the current to animal tissues a very strong external secondary resistance is developed, but it is easy to prevent it from coming into existence by the methods which I give. The internal secondary resistance which has its seat everywhere in moist porous bodies has up to this time only been observed in any great degree in the tissues of living plants, and therefore comes less into consideration in the experiments of which we are treating[2].

The investigation of external and internal polarisation, of external and internal secondary resistance of moist porous bodies which engaged me for many years, was only one link in the series of

[1] Gesammelte Abhandlungen, vol. i. pp. 80–130: 'Über den secundären Widerstand, ein durch den Strom bewirktes Widerstandsphänomen an feuchten porösen Körpern' (Dec. 20, 1860).

[2] For further information on Secondary Resistance, see H. Munk, Über die kataphorischen Veränderungen der feuchten porösen Körper. Archiv für Anatomie, Physiologie, &c., 1873, pp. 241 ff.

researches by which I sought to elucidate the secondary electromotive phenomena in muscles and nerves. Though the pursuit of my chief object was excessively hindered by these preliminary studies, yet my impatience was moderated, not only by the evident necessity of laying a firm foundation to work upon in this department, but also by the consideration that this foundation is equally indispensable for all electro-physiological investigations [1].

I was unfortunately prevented by other problems for nearly twenty years from making use of what I had ascertained. Almost at the same time that I became possessed of unpolarisable electrodes, I had discovered in saline clay an invaluable means of leading currents in or off in electro-physiological experiments, I had given Poggendorff's method of compensation the right form, and somewhat later I added to these advances in methods of research, the invention of the aperiodic galvanometer. It thus became necessary for me to repeat almost all my former experiments with these new and much better appliances, in which measurement of the electromotive force now took the place of mere estimation of the strength of the current. The investigation of the living specimens of Malapterurus from West Africa which were kindly consigned to me by Professor Goodsir of Edinburgh, also took me away from this subject; and, more recently, it has taken me nearly two years to work up the posthumous papers of Dr. Sachs on Gymnotus. The latter interruptions had, however, the important result that I gained some information regarding secondary electromotive phenomena in electrical organs.

6. Preliminary description of Apparatus and Methods.

I defer the detailed description of the apparatus and methods which I now use until I have further communications to make. It is, however, desirable to say sufficient on the subject to render what follows intelligible. In the experiments on muscles the gracilis and semi-membranosus muscles of the frog were commonly used. They were left in their natural connection, and extended in the 'muscle-stretcher [2],' in the way I have employed whenever I desired to work with muscles in an immobilised state. Close to the ivory plates of the stretcher the edges of the wedge-shaped

[1] Cf. Gesammelte Abhandlungen, vol. ii. pp. 191 ff.

[2] Untersuchungen, vol. ii. part i. p. 86. Also Gesammelte Abhandlungen, vol. i. pp. 118, 119, and vol. ii. p. 313.

pads [1] were applied to the internal (that is, femoral) side of the muscles; through these pads the polarising current entered the muscles. Between their edges, the edges of the pads which led off the polarisation current to the galvanometer were in contact with the external side. On account of the resistance of the tendons, which are apt to get dry, it is not feasible to conduct the current to the muscles through the fragments of bone outside of the ivory plates, which would have been in many respects a far better mode of proceeding. Both pairs of electrodes, which in the following pages will be called for shortness sake battery-pads and galvanometer-pads, are covered with clay, which is often renewed.

In consequence of the very small duration of most of the experiments, errors consequent on external secondary resistance are scarcely to be apprehended; at all events, if they exist, they can be readily recognised. The muscle-current was compensated, with the aid of the round compensator, by a derivation-current from a Raoult's battery [2].

In the experiments on nerves the two sciatic nerves of the same frog were commonly used as one. They were secured to the upper surfaces of two pieces of cork with insect needles, and gently extended by shoving the corks along a horizontal glass rod; the two pairs of electrodes were applied in the same way as in the case of the muscle. In the experiments on the roots of the spinal nerves, unpolarisable tube electrodes with clay tips (*Stiefelelektroden*) were sometimes used, at other times special contrivances [3].

A condition essential to certainty of results in these experiments which is difficult to secure, is that of complete insulation of the

[1] Gesammelte Abhandlungen, vol. i. pp. 88, 89.

[2] Untersuchungen am Zitteraal, p. 141.

[3] Since my last publication of an experimental character, a phenomenon connected with the *Thonstiefeln* has come under my notice, which not only deserves consideration in using this form of non-polarisable electrodes, but is on other grounds interesting. If you have a pair of such tubes, the freedom of which from polarisation you have ascertained by bringing the tips into contact, and then touch the thick upper part (*Wulst*) of the one with the tip of the other, a current is found to exist of which the direction is from the tip to the '*Wulst*.' This action is less marked in fresh tubes than in tubes that have been prepared for some time. This may be explained on the assumption that there is an electromotive action between moist and less moist clay, though in a series of layers of clay of different degrees of moisture there is no gradation of tension. Moist clay brought into contact with less moist between zinc pads gives an e.m.f. amounting to 0·014 Raoult. The relation of the electromotive action between clays of different degrees of moisture to the clay thermal currents of Nobili has not yet been explained. (Untersuchungen, vol. ii. part i. pp. 201–203.)

battery-circuit from the galvanometer-circuit, so as to ensure that even when very large electromotive forces are used, such as that of a Grove's battery of fifty elements, the galvanometer remains unaffected when both circuits are open. I have already given shortly the means by which this can be accomplished in the description of my experiments on external polarisation in moist conductors[1]. It consists in breaking both circuits in two places. The contrivance by which this is effected fulfils at the same time another purpose. It enables the observer to determine the time ('closing time') during which the polarising current is sent through the object of polarisation. I possess mechanical means by which I can alter this by continuous gradation from $\frac{1}{1000}$ to $\frac{1}{10}$ of a second, and then go on at intervals of 0·3 second up to 20 seconds. Beyond this the variations may be made by the watch. With the same apparatus I am able to determine the interval between the opening of the battery-current and the closing of the galvanometer-current. This I call the 'transmission time' (Übertragungszeit).

The galvanic apparatus used for polarisation was either a Daniell's battery, of which the elements were of the usual drinking-glass size, and the specific gravity of the dilute acid was 1·030 at 19·4° C., or a Grove's battery of the small elements I use, of which I possess fifty[2]. In order to be independent of the variable resistance of the pads, muscles, &c., the good condition of the battery was controlled by means of a metallic closure. When other electromotors were used, it is specially stated.

The secondary electromotive actions were observed with the aid of the aperiodic galvanometer. As these actions are often in two opposite directions one after the other, the aperiodicity of the instrument has special value. They render it unnecessary to use contrivances such as I formerly employed, by which the galvanometer-circuit was closed after a longer or shorter transmission time, instead of, as now, immediately after the opening of the primary circuit. Finally, it can be readily understood that in experiments on polarisation, as in those relating to electrotonus, it is necessary constantly to watch the condition of the primary current, by means of a special galvanometer. This would only be possible with the Wiedemann

[1] Gesammelte Abhandlungen, vol. i. p. 2.

[2] In the year 1849, the Academy, to which I had not then the honour to belong, was good enough to place at my disposal a Daniell's battery made by Siemens and Halske, of 100 elements, for this research. I soon, however, recurred to the small Groves, which are alike more effectual and more convenient.

galvanometer, it being required to compare in experiments which followed each other immediately, the perhaps permanent deflection due to a current of thirty Groves, with the ten thousand times feebler movement produced by a current of a single Daniell lasting a few thousandths of a second. I lost much time and trouble in the attempt to read the two galvanometers, viz. the one for the polarising current, and that for the secondary current, through the same telescope. Besides the technical difficulties which this involves, the observer is overburdened by having to do too many things at the same time. I therefore recurred to the more simple method of having the second galvanometer read by an assistant.

7. Secondary Electromotive action of muscles in regard to its dependence on the density and duration of the primary current.

Let us suppose the group of muscles, gracilis and semi-membranosus, extended in the muscle-stretcher so firmly that they do not perceptibly move in contraction, and the two pairs of electrodes applied in the manner described, and the muscle-current compensated. If the electrodes are applied symmetrically the muscle current ascends; its electromotive force, although often insignificant, frequently reaches 0·017 Raoult.

If a current be now applied to the muscle for a longer or a shorter time, the galvanometer circuit being 'doubly' open, and if the galvanometer circuit be shut immediately after the battery circuit has been doubly opened, any secondary electromotive action that may have been excited in the muscle equalises[1] itself through the galvanometer circuit, and is truly expressed by the deflection of the galvanometer, provided the compensation remains undisturbed. If the battery circuit is long closed, if the tension of the muscle is diminished, or if strong contraction occurs, this condition is not always certainly fulfilled; and besides, if a strong muscle-current is to be compensated, the contraction leaves an after-effect. The secondary electromotive actions are however generally too marked to be mistaken for such disturbances. They are due to the internal

[1] [When any spot a on the surface of a moist conductor is negative to any other spot b, the current which exists from a to b is said *sich abzugleichen* by currents outside of it which are directed from b to a. The same expression is used of a current which flows from b to a through a galvanometer of which the terminal electrodes are applied to these spots. Whenever possible, the word '*abgleichen*' is Englished by the word '*equalise*.'—Ed.]

polarisation of the muscles alone; and even if external polarisation occurs to an observable degree in the electrodes of the battery, it cannot equalise itself through the galvanometer circuit. Moreover, one may readily convince oneself that every part of the muscles has a secondary electromotive action in the same direction. Consequently, if the resistance in the galvanometer circuit is sufficient, the strength of the action increases with the distance apart of the galvanometer pads. If all parts of the muscle were similar, they must all have an equally strong secondary electromotive action. Apart from the impossibility of applying the electrodes twice successively in the same way, this condition is not fulfilled exactly in our group of muscles, because the semi-membranosus becomes gradually smaller towards its lower part. We shall find, however, another reason why the two halves of a muscle do not act with the same secondary electromotive strength[1].

If currents of different strengths are passed through the muscle for different periods of time, the secondary electromotive actions appear at first very confused. Sometimes negative deflections occur, as if from ordinary moist porous bodies susceptible of internal polarisation, sometimes, on the other hand, positive deflections, as if external polarisation was mixed up with it. As already remarked, this last is impossible with the arrangement used. It therefore appears that the positive secondary electromotive action depends upon positive internal polarisation, a condition of which the series of bodies which I tested as regards their internal polarisability[2] gave no example. This positive internal polarisation of muscular tissue is therefore the point of novelty and interest, and it is most important to establish the conditions under which it appears.

There is no other way of accomplishing this but by making a table with double entry, in one column of which, let us say the horizontal one, the time of closure is entered, and in the vertical column the number of battery-cells. In the space corresponding to a given time of closure and a given density of current, must be entered, 1st, the deflections which the polarising current creates in

[1] Gesammelte Abhandlungen, vol. ii. pp. 161, 315, 575.

[2] I first gave information about it in my 'Untersuchungen,' vol. i. 1848, p. 240, and vol. ii. part i. 1849, p. 331. In 1852 I made a detailed communication upon it to the British Association in Belfast (Report of the twenty-second Meeting of the British Association, &c., held at Belfast in September, 1852, London 1853, Notices and Abstracts, p. 78). Later I alluded to it in the Report on the 'Zitterwelse' from West Africa (Monatsberichte der Akademie, 1858, p. 106), and in the Untersuchungen am Zitteraal, p. 206.

the galvanometer (P); 2ndly, the resulting secondary electromotive action shown by the galvanometer (S), and both effects in the ascending as well as in the descending direction of the polarising current. It is a most tedious business to compile such a table. The secondary actions created by the stronger and longer currents are generally so persistent that one almost requires a fresh preparation for each experiment. The only exceptions are the cases where quite weak currents last only for a small fraction of a second, as then the polarisation is transitory enough to allow of other experiments, especially with stronger and longer currents to follow them immediately. On the other hand, those cases are also exceptions, in which a current of long duration creates so persistent a polarisation, that the battery-circuit can be opened and the galvanometer-circuit closed for a short time without perceptibly altering the condition of polarisation. In the other cases where a polarisation, sinking at first rapidly and then slowly, remains behind, it would no doubt be easy to compensate afresh and so produce equilibrium in the galvanometer-circuit. But in repeated experiments in the same preparations one would not be sure of getting the same secondary action as in fresh muscle. If one waits till the polarisation disappears, too much time elapses for it to be assumed that the muscle will behave like a fresh one. On account of the necessity of leaving the pelvis attached to each group of muscles, each frog furnishes only one group, so that every experiment which does not come under these two exceptions requires a new frog. But if the results are to be comparable, it is necessary that, firstly, the frogs should not differ too much in size; and, secondly, that they should be as much as possible in the same condition. If it is remembered that in order to arrive at a fairly complete knowledge of the phenomena it is necessary to try at least ten times of closure and as many current densities in both directions, which correspond to two hundred experiments; that these two hundred experiments must be made successively on almost as many frogs, which must be as far as possible equally fresh and large; and if in addition to this the unavoidable failures and repetitions are taken into consideration, it is seen that a table such as is required is the work of several weeks in which a great number of favourable circumstances must be present, so that no one will be surprised that in so long a time I only attempted it twice.

The first time, in the autumn of 1855, I possessed none of the new apparatus or methods of experiment, and I knew as yet

nothing about secondary resistance. It was indeed on this occasion that I discovered it, though unfortunately too late, and the whole work, which would however now be behind the time, had to be thrown aside. I succeeded for the first time last summer, 1882, in working out a new table. Meanwhile the difficulties had not decreased, for in proportion as the means of assistance were perfected the demand for accuracy had increased also. I took as the normal measurement of a frog 22 centim. from the tip of the nose to the end of the longest toe. I never allowed a greater variation than ½ a cm. I employed 14 times of closure from 0″·006 to 25′, and 9 strengths of current from 1 Daniell up to 40 Groves' cells. Not counting the faults and repetitions, the number of experiments was 198. The present paper would not be a suitable place in which to reproduce the entire table. I will only give one example of it.

		0″·006	0″·076	0″·320	1″·122	4″·626	10″·022	14″·754	20″·018	1′	5′
↑	S	+86^{sc}	+133	+109	+84	+73	−66	−79	−125	−170	−119
	P	18^{sc}	109	400	305	1250	020	2100	2216	1669 to 1824	1824 to 1962
X											
	S	+79	+111	+160	+164	−15 / +4	−9 / +34	−87 / −112	−62	−100	−24
	P	14	178	229	865	2129	1337	2412	1777	1657 to 1860	1860 to 2151
↓											

It is hardly necessary to say that the headings in the top row show the time of closure, under one second before the first and under one minute before the second of the double perpendicular lines. The X means that the polarising-current is produced by 10 Groves. The arrows indicate the direction of the current in the muscle. The horizontal rows S contain the deflections caused by the secondary current. The plus mark indicates positive, the minus mark negative polarisation. The sensitiveness of the galvanometer (*S*) was diminished, only one bobbin at a distance of 3 cm. being employed. Two numbers bracketed represent polarisation in two directions. In the horizontal rows P, are found the deflections due to the primary current. As 4″·626 is greater than t max.[1], the mirror of the galvanometer (*P*) as deflected by the primary current, reaches, whenever the time of closure is equal to 4″·626 or exceeds it, the deflection at which it would have been held by a continuous current. The magnitude of the foregoing numbers

[1] Gesammelte Abhandlungen, vol. i. p. 302.

depends on the fact that the deflections are reduced. The galvanometer is so graduated that the relative rotating moment of the bobbin was known for each 5 mm. of distance. In proportion to the strength of the current the galvanometer bobbin was placed at such distance from the mirror that it produced a suitable deflection A. Suppose m to be the relative moment for 20 mm. distance of bobbin, m' the moment for the distance chosen each time, the reduced deflection $A_r = A\frac{m}{m'}$. With the strongest currents were obtained reduced deflections of nearly 10,000 divisions of the scale (see Sect. 6). In the numbers in row P of the table the great imperfection attaching to these experiments notwithstanding all my trouble, is seen. From the time of closure $4''{\cdot}626$ onwards the collective deflections through the primary current should have been the same. They vary in a ratio of 100 : 180, partly from the impossibility of making the resistance of the muscles and the wedge-shaped pads with their clay tips the same size in several consecutive experiments, and (for this explanation is hardly sufficient) partly on other unknown grounds. The increase of the strength of the current, when the closure lasts one minute or more, arises from the warming of the pads, of their edges, and of the muscles themselves. With greater strength and longer continuance of the current, this action is more than balanced by external secondary resistance at the point where the current enters the muscle. The polarisation after 1′ closure was so constant that after a short time of opening the battery circuit the galvanometer circuit could be closed without perceptibly altering the condition of polarisation, so that it was unnecessary to use a new preparation (p. 169).

8. Graphic representation of the Polarisation curves in relation to the time of closure; Discussion of the same.

However incomplete these experiments may be, a number of important conclusions may be drawn from them. The subjoined Fig. 5 shows shortly the general course of the phenomenon. Let T be the time of closure, Δ the density of the primary current, $\pm s$ the strength of the secondary electromotive action, then the plane seen in perspective like a boarded floor, is the T-Δ-plane. At the points of this plane corresponding to the given times of closure and the given densities of current, the secondary actions are set off parallel to the

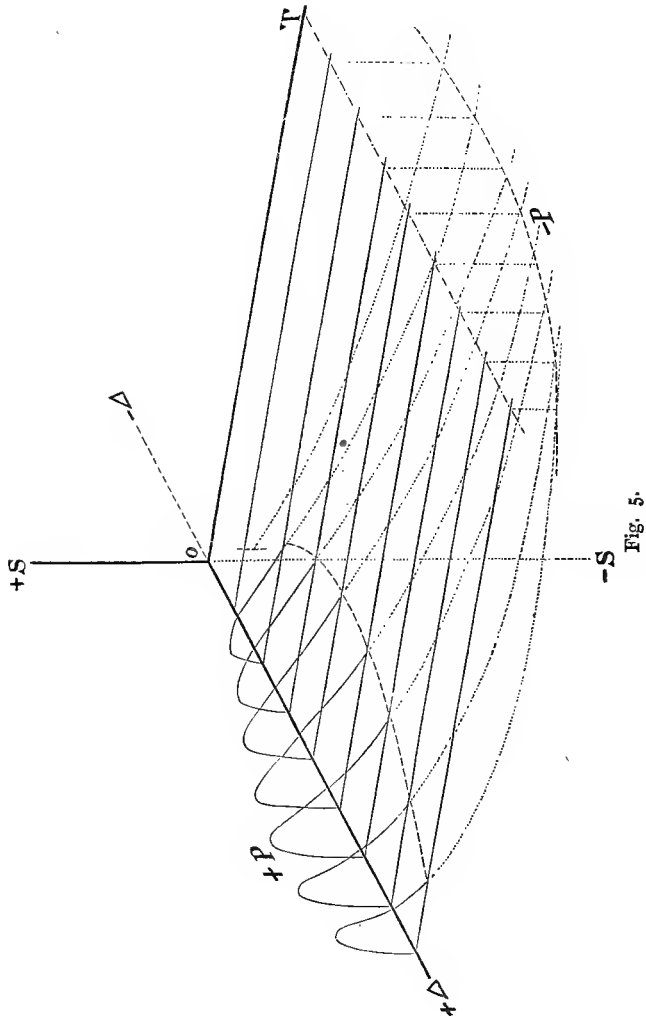

Fig. 5.

S-axis, the positive above and the negative below the plane. The ordinates s themselves are not drawn, but the curves connecting them corresponding to a definite density of current are drawn. These therefore represent the strength of the secondary action due to this density of current as a function of the time of closure. Although these curves have similar courses they alter continually with increasing density of current. They agree in the following general characters. The zero time of closure corresponds naturally to the zero of secondary action, consequently the curves themselves start from the Δ-axis. Each curve rises quickly to a positive maximum, and then sinks less rapidly but still very fast to the T-Δ-plane. These curves are drawn in the figure up to the point where they intersect this plane as unbroken lines, beyond this in their negative course they are represented by dotted lines. Here appears a negative maximum which is generally less clearly marked, and is at a greater distance from the point of intersection than the positive maximum, though this distance diminishes with increasing density of the current. Thus it occurs with 1 Daniell only after 15′, with 1 Grove after 10′, with 2 Groves after 5′, with 5 Groves after 1′, &c. It lies at 1′ in the part of the table shown, which was obtained with 10 Groves, and it is obvious that it cannot depend at all on the weakening of the primary current by secondary resistance. I have not followed the polarisation-curves further than this negative maximum. However, they probably present nothing particular, but approach very gradually the axis of the times of closure, till from the excessive duration of the experiment the results are obscured by all kinds of collateral actions.

With a current density of less than 2 Groves and with a very short time of closure there is generally no polarisation appreciable by the galvanometer. The first traces observed with 1 Daniell and 1″ time of closure, are negative; internal polarisation of the muscle is also obtained as I have long ago described, by passing a current comparable with its own for a long time through it[1]. The first positive traces appear for the first time with 2 Groves and about 0″·3 time of closure.

The time of closure at which the positive polarisation passes into negative may be called the critical time. In the figure, the points at which the polarisation-curves described on the time of closure intersect the T-Δ-plane, are connected together by a curve drawn with an interrupted line. This curve is therefore

[1] Gesammelte Abhandlungen, vol. ii. pp. 191, 192.

that of the critical times of closure with the axis of current densities as abscissal axis. It is obvious that the curve of the critical times of closure has a maximum; in my experiments this maximum lay somewhere between the density of the current generated in 2 Groves, and the critical time of closure then reached was about 5″. With 20 Groves it was only about 1″. If the positive maxima of the individual polarisation-curves are connected by a curve, this curve also shows a maximum with from 20 to 30 Groves; and similarly a curve which unites the negative maxima exhibits a maximum, but does so with 1 Grove only.

It remains to give an idea of the amount of these maxima as compared with that of the muscle-current. If I pass through a galvanometer-circuit, in which the group of muscles have been placed as if for a polarisation experiment, an electromotive force of about 0·045 to 0·055 Raoult corresponding to the force of the whole[1] artificial transverse section of the gracilis or semi-membranosus, there follows a deflection of 235–285^{sc}, the sensitiveness of the galvanometer having been diminished. I noticed the strongest negative polarisation after closure of a current of 1 Grove for 10′, and it gave 423^{sc}. I obtained the strongest positive polarisation by closure of 20 Groves during 0″·075; it amounted to 239^{sc}, and therefore appeared to have less electromotive force than the muscle-current. We shall soon see, however, that this is a deceptive estimate. What the relation is between the secondary electromotive actions in muscles relatively to their size, and those of other moist porous bodies, has not yet been investigated.

So far as the above numbers for the position of the maxima, &c., depend on the density of the primary current, they are only applicable to the particular group of muscles in frogs 22 cm. long, with our method of conduction. Moreover Fig. 5 must not be understood to represent the relation between the numerical values. The available space rendered this impossible. As, for instance, the critical time of closure in our experiments reached at most 5″, and the maximum of negative polarisation first appears only at 10–15′, the figure would require to be from 3 to 4 metres long in order to show this maximum at the right place with the same proportional measurement as that adopted for the first few seconds. The current densities would require at least five times as broad a space, &c.

[1] Gesammelte Abhandlungen, vol. ii. pp. 193, 243.

Closely connected with experiments on galvanic currents of variable strength and duration, are experiments made with electromotors, which from their nature produce short sudden shocks. These produce positive polarisation at once. I have not yet found time to pursue this kind of experiment with new means and apparatus, and must content myself with citing older results, which are in the main correct.

In December, 1846, I obtained to all appearance positive polarisation in the legs of a living frog with a Saxton's machine, the shocks of which could be sent in the same direction by a commutator (*Stromwender*). As this machine[1], constructed for Dove by Oertling, passed into the possession of the Physiological Institute, I am in a position to control those experiments which were performed with very imperfect knowledge and experimental methods. Under somewhat better conditions, in November, 1855, I observed positive polarisation in the group of muscles with opening shocks of the induction coil. Lastly, as early as December, 1846, I observed positive polarisation in frogs which I killed with a heavily-charged Leyden battery having a surface of about 0·31 square metres. The muscles looked blood-stained (*blutrünstig*), and only gave traces of reaction on the application of other shocks[2].

9. On the curves of Polarisation in relation to the time after opening the Primary Current.

The polarisation of muscles can still be studied in relation to the course it takes after the opening of the primary current, and this course may be represented by a curve drawn relatively to the time which has since elapsed. This period of time may be called the 'opening time.' In general the positive as well as the negative polarisation appears very persistent. In Sect. 7 I have already alluded to the difficulties which arise each time that one wishes to employ the same muscle for several consecutive experiments. After a muscle has been strongly polarised in a positive direction it may require twenty minutes or more to elapse before it has so far regained its original condition that the alteration may be disregarded. As, besides, without having been polarised, the muscle does not during this period retain its electromotive condition unaltered, it is

[1] Untersuchungen über thierische Elektricität, vol. ii. part i. pp. 398 ff.; Wiedemann, Die Lehre vom Galvanismu su. Elektromagnetismus, vol. ii. 2 ed. Braunschweig, 1874, p. 236.

[2] Untersuchungen, *loc. cit.* pp. 181, 182.

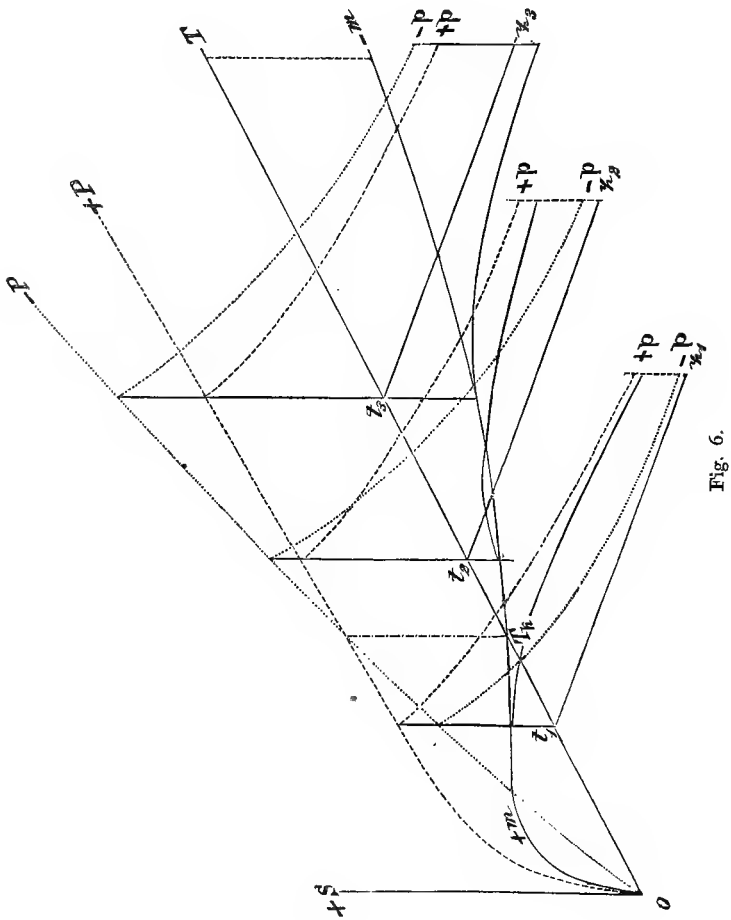

Fig. 6.

never possible to say if or when the restoration is complete. The same thing occurs with negative polarisation. Polarisation curves, however, drawn relatively to the opening time, present other important peculiarities. If the opening occurs at the critical time there often follow deflections in two opposite directions, corresponding first to negative and then to positive polarisation. The transition from purely positive polarisation to purely negative, through such double action, may be explained in the manner expressed by Fig. 6. It must not be imagined that from the opening of the primary circuit to the change of sign of the polarisation, the action is simply positive and then simply negative. It is much more likely that both are present from the moment of closure, and increase in accordance with a different law, by which the negative polarisation increases more in proportion to the time of closure, while the positive rises first quickly and then slowly. In the figure this is represented on the vertical plane, which is seen in perspective stretching from left to right backwards. In this plane the abscissal axis $o\,T$ is the increasing time of closure, the broken curve from o to $+\,P$ is that of the positive polarisation for a given density of current, the dotted one from o to $-\,P$ that of the negative polarisation for the same density drawn relatively to the time of closure. If the ordinates of these component curves[1] are summed up algebraically, and the result inscribed according to its positive or negative value above or below the abscissal axis, you have the resulting curve $o\ (+m)\ T_k\ (-m)$, which at T_k, the critical time of closure, intersects the abscissal axis $o\,T$, and in fact is nothing but one of the polarisation-curves drawn with reference to the time of closure such as we had in Fig. 5. The negative maximum, with a longer time of closure, is explained by the supposition that the curve of negative polarisation either begins to sink, or rises more slowly than the positive, or that the latter begins to rise more quickly (Sect. 11 and 21).

On vertical planes which meet at a right angle the S-T-plane of the polarisation-curves, drawn relatively to the time of closure, the component polarisation-curves are represented relatively to the time of opening; the abscissal axes $t_1\,z_1$, $t_2\,z_2$, $t_3\,z_3$ represent in each case the increasing time of opening. The polarisation-curves drawn relatively to the time of opening are treated in a corresponding way to those of the time of closure, from which they proceed. The component positive ones are shown by interrupted lines, the component

[1] Cf. Untersuchungen am Zitteraal, p. 215.

negative by dotted lines, the resultants by continuous lines. In this representation the assumption is made that positive polarisation declines more slowly in time, and negative more quickly. A glance now at the figure shows that if the primary current is opened at the time t_1 the polarisation will always remain positive. On opening it at the time T_k, if one could hit this time, the polarisation would be nil for the first moment and then positive. If, however, it is opened at the time t_2 a double action follows, first negative and then positive. Further on at t_3 the negative polarisation, which increases more in proportion to the time of closure, has risen so high above the positive, which has remained nearly at the same height as at first, that notwithstanding the more abrupt descent of the negative curve the curves no longer intersect each other, and purely negative polarisation appears.

Besides the actions in two opposite directions which can be so satisfactorily explained, there occur in the successive phases of the polarisation-currents peculiarities, which, inasmuch as they do not occur regularly under definite conditions, are difficult to indicate with certainty. In a few cases, polarisation in opposite directions occurs with a first positive and second or principal negative deflection. Often the polarisation increases very slowly, which probably depends on the disappearance of the opposite kind. Frequently,

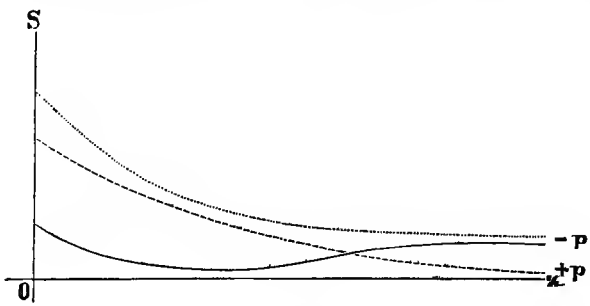

Fig. 7.

indeed, the actions are in one direction only, but double in so far that the deflection first reaches a maximum then sinks to a minimum, and then once again rises to a maximum which often even exceeds the first. A case of the sort is seen in the preceding table, with a descending current, and 14″·754 time of closure. This is explained by the circumstance that the two component curves, drawn relatively to the time of opening, take such a course that the one is completely above the other, but is more convex

towards the abscissa, so that it first approaches the lower curve and then separates from it, as shown in Fig. 7. It is impossible here to follow further these particulars which are still very imperfectly investigated. The most important result from them consists in the necessity of assuming the coexistence of both polarisations in muscle, from which it follows that the apparent magnitude of the resulting positive or negative polarisation teaches us nothing of the true magnitude of each of the component polarisations, for the result we obtain represents the difference between the two components, either of which components may be greater than the difference itself.

10. On the Influence of the Direction of the Primary Current on the Secondary Electromotive Action of Muscles.

I pass over the casual observations and the long list of preparatory experiments which led me at last to the view that in a regular muscle, for instance our group of muscles, the upper half exhibits stronger positive polarisation in an ascending, and the under in a descending direction. The best means of proving this consists in sending the primary current alternately in both directions, first through one half of the muscle and then through the other, allowing exactly the same period of time to elapse between each momentary current, in which case polarisation disappears with the exception of a small residue which is then compensated. If its complete disappearance is waited for, so long a pause becomes unavoidable after each experiment, that great inconveniences arise. If you wait on each occasion, without reference to time, till the polarisation reaches a certain or absolute value, that is to say till it either sinks to a fraction of its original value or to a certain number of divisions of the galvanometer scale, or 'degrees of the compensator,' all kinds of uncertainties are met with. With a short time of closure, and a strong current, the first method of experiment always gives the best result. In any case it is to be preferred to the statistical method which consists in obtaining a mean value for the positive and negative polarisation in both halves, by experiments on constantly renewed muscles, so that the current is only once passed in one direction through each half of the muscle. The variations in the strength of the primary current due to irregularities in conduction are, as we have already seen (Sect. 7), so considerable in spite of every care, that for their compensation an enormous number of experiments would be necessary.

But even when the battery-electrodes are applied to one and the same half of the group of muscles, we cannot be sure that the primary current is equally strong in both directions. As is well-known, there is no such law of reciprocity for electric currents as there is for rays of light. The same electromotive force, acting in opposite directions through the same series of conductors, often generates currents of very different strengths. The necessity of seeing clearly into the conditions of the irreciprocal conduction of electric currents gave occasion to some experiments of von Beetz and myself, which again were the germ of Professor Christiani's thorough investigation of this subject[1]. I have convinced myself that a perfectly sufficient reciprocity of conduction occurs through a clay rod through which the current is led as through a muscle.

This general experience must not, however, be depended upon, but care must be taken to note the strength of the primary current along with that of the secondary. Professor Georg Quincke, then still in Berlin, had the great kindness to help me with the older observations of this sort, while latterly Professor Christiani aided me, to whom I owe my warmest thanks for his assistance in the present organization of my experiments.

The following table gives an idea of the great differences which exist between the two halves of the muscle. It is to be understood that one of the galvanometer electrodes is applied close to the equator of the group of muscles, and the other invariably either over the under, or under the upper battery-electrodes.

TEN GROVES.—TIME OF CLOSURE 0″·320.

1. *Upper Half.*

Muscle current: 189sc, 21cgr ↓.

S ↑	+113sc	+ 93	↑ +145	+ 81	↑ +159	+ 64
P	171sc ↓	169	153 ↓	159	180 ↓	190

2. *Under Half.*

Muscle current: 214sc, 22·5cgr ↑.

S	+294	↑ +199	+285	↑	− 3	+255	↑	− 9
					+136			+ 92
P ↓	200	160 ↓	160		169 ↓	185		180

3. *Upper Half repeated.*

Muscle current: 264sc, 27cgr ↓.

S	+ 34	↑ + 87
P ↓	210	220

[1] Arthur Christiani, Beiträge zur Elektricitätslehre; Über irreciproke Leitung elektrischer Ströme, Berlin, 1876.

4. *Under Half repeated.*

Muscle current: 285^{sc}, 30^{cgr} ↑.

S	↑	− 16	+ 142
		+ 38	
P		190 ↓	190

The total of the ascending positive polarisation in the upper half of the muscle is 504, that of the descending 272. For the lower half the corresponding numbers are 976 and 465. The numbers in themselves are, I may incidentally remark, not to be compared with those mentioned in the previous table, as on this occasion the bobbin of the galvanometer was close up.

One glance at the table shows that the excess of positive polarisation cannot be supposed to be attributable to oscillations in the strength of the primary current. These oscillations, which arise in part from defects in the apparatus for regulating the time of closure, are sometimes not apparent, sometimes they have the opposite direction to that which would arouse suspicion, and even when it is otherwise they are much too small to give any grounds for suspicion. Moreover, such an explanation is opposed by the cases of which the table offers three, in which, though the direction of the polarising-current is less favourable to positive polarisation, a preliminary negative deflection appears, and further the not infrequent cases in which the polarisation is purely negative; for provided the time of closure is equal, either action in two opposite directions, or negative polarisation, imply the existence of a stronger polarising-current. These cases exclude the idea that we have to do with a phenomenon of resistance.

Another conjecture which offers itself here deserves, however, serious consideration. The whole phenomenon might rest on a deception. As we would expect from the law of the muscle-current, and as is evident from the table, as regards the foregoing case a descending muscle-current prevails in the upper, an ascending one in the lower half of the muscle. The negative variation and its after-effect are manifest in the upper half as ascending, and in the lower half as descending electromotive action. Consequently the after-effect in the upper half of the muscle, with an ascending polarising-current, will reinforce the positive polarisation, and with a descending one will diminish it. In the under half *mutatis mutandis* the same will happen. Now since the muscle contracts at the passage of the polarising-current, everything might thus be explained on old well-known grounds without having recourse to anything new.

I believe I have demonstrated in two ways that this explanation, although conceivable, is not correct. I first formed an idea of the magnitude which the after-effect would here attain. Instead of the polarising battery, I allowed the mechanism, which regulates the time of closure and of the 'transmission time' (*Übertragungszeit*), (Sect. 6), to close the primary current of the inductorium. I left the nerve still attached to the group of muscles and laid it on the platinum plates of my electrodes (*stromzuführende Vorrichtung*)[1]. By the action of this mechanism, the muscle was thus, instead of being polarised, tetanised for the fraction of a second, and between the end of the tetanus and closing of the multiplier circuit, the same transmission time intervened as between the end of the polarising current and the closing of the multiplier circuit. The result of several experiments which, according to the standard of that time were perfect, was that when this method of experimenting was used, only traces of after-effect were visible, and were by no means sufficient to explain the observed differences of polarisation. Indeed this might have been predicted, for the after-effect increases with the duration of the tetanus which here only lasted a very short time.

Secondly, I cut the muscles at the equator about half through their thickness so that there was a gaping wound which behaved as an artificial transverse section. The wedge-pad, which was usually applied to the equator, was now applied to the wound. The muscle-current now had the reverse direction in both halves, and consequently the negative variation was also reversed. Yet now, as formerly, the ascending positive polarisation predominated in the upper half of the muscle, and the descending one in the under half.

If I consequently considered it proved that the positive polarisation in both halves of the muscle is stronger in the direction from the equator to the ends than in the other direction, this is equivalent merely to a statement of the phenomenon actually observed, a phenomenon which admits of more than one interpretation. If we call the positive and negative polarisation generated by the ascending current respectively $P\uparrow$, $\Pi\uparrow$, the corresponding polarisation from the descending current likewise $P\downarrow$, $\Pi\downarrow$, then the state of matters is this, that not $P\uparrow - \Pi\uparrow = P\downarrow - \Pi\downarrow$, but that in the

[1] Untersuchungen über thierische Elektricität, vol. i. p. 450. It was in March, 1857, before 'physiological' salt clay and unpolarisable electrodes were in use. The muscle current was observed by the nerve-multiplier.

upper half of the muscle the left, and in the lower half the right term is the greatest. Naturally this can occur from many combinations of positive and negative alterations of the four terms, upon two of which, however, we must especially fix our attention. It is either $P\uparrow \gtrless P\uparrow$ or $\Pi \lesssim \downarrow\Pi\uparrow$; the upper sign applies to the upper, the under one to the lower half of the muscle. What is actually the case will be decided further on with some amount of probability.

A remarkable fact which is also expressed in the table, is the greater strength of all secondary actions in the lower half of the muscle. Neglecting the negative preliminary deflections, the sum of these actions in the upper half amounts to 776^{sc}, that in the lower half to 1341^{sc}. The corresponding numbers for the primary current are 1452 and 1434^{sc}. The difference of the secondary actions is not explained by the downward tapering form of the semi-membranosus, for I have observed it also in the symmetrically-formed gracilis. With the electrodes of the galvanometer applied symmetrically to the group of muscles, one would expect to obtain with alternately ascending and descending polarising-current, a stronger positive polarisation in a descending than in an ascending direction. This I in fact observed in January, 1857, with less perfect apparatus indeed, but with sufficient distinctness.

The observation is important, that in the series of experiments here described, when they lasted long their result became uncertain, and finally often became opposite; so that, for instance, in the upper half of the muscle not only is the descending positive polarisation stronger, but negative polarisation appears even with an ascending primary current. Finally, one circumstance deserves to be mentioned which comes out so distinctly in the table that I must consider it as unquestionable in spite of its paradoxical nature. With very strong descending currents the polarisation in the whole group of muscles becomes positive again after the critical time of closure, which is as usual marked by deflections in opposite directions. With 20 Groves there was only at first a trace of this condition; with 30 Groves it was stronger; with 40, however, so distinctly marked that with an ascending current and times of closure respectively, 20″, 1′, 5′, I obtained deflections of -125, -112, -170^{sc}; with a descending current, $+165$, $+166$, $+117^{sc}$. Whether this is connected with different polarisability of the two halves of the muscle in both directions, and how it is so, is still quite obscure. In order to embrace the relation in Fig. 5,

the curves should have been drawn from the $(-\Delta)$ axis beyond the T-axis. This was the less worth while that it is now apparent that such a double figure would be necessary for each half of the muscle.

Polarisation experiments, with cross direction of the primary current in muscle, are made with great difficulty, and have not yet been satisfactorily carried out.

11. On the Influence of various circumstances on the Polarisation of Muscles.

The fact chiefly to be insisted upon is that internal positive polarisation of muscles is only found in the living condition.

I had formerly stated that internal negative polarisation still existed in boiled muscles[1]. This was an error of which I became conscious afterwards, when I experimented on single muscles instead of entire limbs. The internal polarisability of frog's muscle is destroyed by scalding, and completely annulled by boiling. Nevertheless, strong internal negative polarisation is found in an entire boiled frog's leg as I had already rightly observed. On closer investigation, however, it was seen that while the muscle itself was entirely inactive, this polarisation had its seat in the knee joint, that is in the bones or ligaments, or both. The ankle joint of a boiled leg was also found to be strongly polarisable. In the case of the entire limb, the muscles of the limb serve only as conductors to the joint.

Muscles which have been killed in other ways,—beef from the butcher, frog's muscles which have lain forty-eight hours in a moist chamber, or in water, or which have been dried over chloride of calcium and then been softened again—only indicate on the galvanometer slight traces of internal negative polarisability with a current of fifty Groves.

Scalding and boiling therefore exercise a remarkably destructive influence on internal polarisability of the muscles. At the same time, I found in September, 1855, that boiling materially lessened the peculiar resistance of the muscle, which fact has been thoroughly investigated since by Joh. Ranke[2]. Whether this fact and the destruction of internal polarisability of muscles by boiling are connected with each other we shall see further on (Sect. 21).

I think I have remarked that the long continued passage of a

[1] Untersuchungen über thierische Elektricität, vol. i. pp. 378, 379.

[2] Joh. Ranke, Tetanus. Eine physiologische Studie, Leipzig, 1865, pp. 10, 19 ff.

very strong current destroys polarisability. This would explain why a maximum of negative polarisability appears the earlier the greater the density of the current. However this may be, I have in my note-book cases where, in spite of the destruction of polarisability by a strong current, the muscle still contracted. From the incompleteness of my former experiments, I am, however, not sure of these things, and I simply mention them now to show how much has yet to be investigated.

Between saline solution and muscle, positive polarisation is developed in the same manner as between this solution and other animal tissue (Sect. 4). A slice of beef in which the current only reaches a moderate density gives between saline pads only positive polarisation, but a long thin strip gives polarisation in successively opposite directions, or slight purely negative polarisation, for then the internal negative polarisation makes its appearance along with the external positive polarisation.

We have seen above (Sect. 8) that the limbs of a living frog are capable of internal positive polarisation. I early tried similar experiments on living men. In the years 1845 and 1846 I procured a powerful voltaic pile of the very earliest fashion consisting of 150 zinc-copper double plates. Of these, 100 pairs were circular having a diameter of $1\frac{1}{2}''$, 50 were square being $2\frac{1}{2}''$ long each side. When the pile was used, disks of paper pulp steeped in a warm tolerably strong solution of chloride of ammonium, were employed as moist conductors to lay between the plates. With the last zinc plate a copper plate was connected, and with the last copper plate a zinc one, each of which was dipped in a basin with saturated solution of salt. The equality of the two forefingers with regard to their electrical condition was first tested by dipping them in the conducting vessels of the multiplier. Of course I met here with the same difficulties as in the experiments on negative variation through voluntary tetanus[1]—difficulties which have since been overcome by the method of compensation. The index fingers were now dipped in the basins connected with the battery in order to receive the shock, and immediately transferred to the conducting vessels in order to observe the secondary electromotive action. The shocks of the battery were no trifle. When received with the whole hand they were felt up to the shoulder, and during the time

[1] Monatsberichte der Akademie, 1852, p. 111; Moleschott's Untersuchungen zur Naturlehre des Menschen u. der Thiere, 1857, vol. ii. p. 247; Untersuchungen über thierische Elektricität, vol. ii. part ii. pp. 186 ff.

the current lasted those sensations of heat and cold were experienced which J. W. Ritter made the subject of his speculations in the beginning of the century[1]. The friends of my youth, Wilhelm Beetz, Ernst Brücke, Karl von Erlach, J. G. Halske, Gustav Karsten, shared then with me the difficulties of these experiments. I am happy to be able here, after nearly forty years, to render them my thanks. The result was at first an irregular confusion of positive and negative deflections, but it was soon possible to control the phenomena. With a short closing of the battery, there followed a positive polarisation, and with a long one (15″ was all that could be endured) a negative polarisation. With a moderately long closure and rapid transference of the fingers from the battery basins into the conducting vessels, negative polarisation followed, and when the transference was slow, positive polarisation.

The actions were strong enough to try if they would not make themselves apparent in a rheoscopic thigh. This was in reality the case. According to Humboldt's method[2], the nerve had two pieces of beef laid on it as conductors; if I touched these with my fingers after I had polarised myself in the battery circuit, the leg contracted most vigorously. As one cannot succeed in making the frog's leg contract by means of voluntary tetanus it is rather interesting that it can be done by secondary electromotive action. Experiments in polarising the human body by means of the shocks of a Leyden battery were without result. On the whole these facts seem to be in complete accordance with those in frog's muscles and in living frogs. Unfortunately so much uncertainty attaches to them that it for the present deprives them of value. I was not then aware of the polarisation at the surface of contact of electrolytes. I only looked to see whether the fingers, after the closure of the battery, had an acid or alkaline reaction like the ends of a frog through which a current was passed, and I found once after long closure, traces of acid reaction on one finger, though they appeared to me to be too slight to lay further stress upon them, more especially as intentional soiling of the fingers with dilute nitric acid and liquor potassæ produced no actions comparable to those which we have to explain. I cannot now, however, understand why I did not alter the experiment so as, for instance, to

[1] Untersuchungen, vol. i. pp. 356, 357.

[2] Versuche über die gereizte Muskel und Nervenfaser, Posen und Berlin, 1797, vol. i. pp. 35 ff.

take the shock with the forefinger while the secondary electromotive action was led off by the middle finger. Until the experiment has been successful in this or some similar form, it is open to the suspicion that we have here to do with external positive polarisation in the skin, and not with internal polarisation of the muscles; on the other hand there is no apparent reason to doubt that the negative deflections observed in these experiments depend upon true internal polarisation, and this new action of the current in the human body appears to me to be in some degree worth the attention of electro-therapeutists. I cannot yet say whether the contraction of the rheoscopic frog produced by polarised human limbs arose from positive or negative polarisation.

12. Positive internal Polarisation of Muscles in Conflict with Tetanus.

One of the most remarkable relations shown by the internal positive polarisation of muscle is, that it is influenced by the state of activity of the muscle, and in reality a tetanised muscle is capable of less strong polarisation than one at rest.

The experiment is a difficult one on account of the negative variation which is mixed up with it, which cannot always be estimated with certainty. The galvanometer electrodes must be applied to the group of muscles to which the nerve is left attached in such a manner that the muscle-current is as weak as possible; then the negative variation is also weak. On account of the asymmetrical construction of the semi-membranosus, a more or less strong ascending current is present when the position of the electrodes is symmetrical (Sect. 7). Hence, we obtain the desired equality by applying the lower electrodes higher up on the muscle. The group of muscles must be so firmly stretched that they do not perceptibly shift on being tetanised. The amount and direction of the remaining variation is noted. We then send a polarising shock of short duration through the group of muscles every minute and a half to two minutes, thus leaving it alternately at rest and tetanised. We regulate the direction of the current so that the negative variation is added to the secondary electromotive action. In spite of this, the action is always less during tetanus than during the repose of the muscle.

The following table gives an example of this behaviour :—

SEPTEMBER 11, 1855.

Muscle Multiplier, Platinum Electrodes in saturated solution of common salt, Common Salt wedge-pads with albuminous films. Twenty Groves.—Time of closure about 1″. A minute and a-half between the experiments.

No.	*Tetanus alone.*	*Ascending polarising current.*		
		Alone.	*With Tetanus.*	Δ
1	5° ↑	—	—	—
2	—	+53°·5	—	+18°·5
3	—	—	+35°·0	−1·0
4	—	+36·0	—	+19·5
5	—	—	+16·5	—
6	—	—	+9·5	−3·0
7	—	+12·5	—	—
8	1·5 ↑	—	—	—

The strength of the primary current was not noted, but the resistance of the immobilised tetanised muscle, according to my experiments, diminishes a little [1].

My note books mention no precautions to ensure that tetanus should always last the same length of time, and that the current should commence an equal time after the beginning of the tetanus. With the knowledge and means we now possess it would naturally be easy to obtain much completer numbers than the above. As they stand they appear to leave no doubt regarding the thesis I have propounded.

I have made similar experiments with negative polarisation. On certain grounds I thought that this polarisation would not be altered by the state of activity of the muscle. On account of the weakness of the positive polarisation subtracted from it, it should therefore appear stronger. Unfortunately, in testing whether it be so or not, we meet with the difficulty that it requires a time of closure of at least 10″ to obtain adequate negative polarisation. As tetanus begins earlier and must last longer than the polarising current, the muscle is affected to such an extent that one generally succeeds in seeing nothing but a rapid subsidence of all action. However, I

[1] Untersuchungen über thierische Elektricität, vol. ii. part i, 1849, pp. 74 ff. When this sheet of my work was printed, Helmholtz' researches, 'Über die Wärmeentwickelung bei der Muskelaction' (in Joh. Müller's Archiv für Anatomie, &c. 1848, pp. 144 ff.) had not yet appeared. I should otherwise have had grounds for considering the possibility that the diminution of resistance which I had observed depended on the action of warming the muscle. I discovered the acidification of muscle by contraction much later.

think I have before me in my rows of figures traces of what was anticipated which can hardly depend on mere chance.

Finally, it is to be noticed that it is not accurately understood in what respect an ordinary experiment on positive polarisation and an experiment on positive polarisation in conflict with tetanus differ from each other. For in experiments without tetanus the muscle is also in contraction during the passage of a short current. The time has not yet arrived to examine this question. Perhaps the apparently smaller positive polarisability of the tetanised muscle depends upon the fact that the tetanus, which lasts longer than the closure of the battery partly arrests the positive polarisation.

13. On Secondary Electromotive Phenomena of Nerves.

When I made a communication to the British Association in Belfast, in the autumn of 1852, on secondary electromotive actions of muscles and nerves (Sect. 7), I had not yet succeeded in obtaining positive internal polarisation in nerves. In connection with my hypothesis regarding electrotonus, and considering the fact that muscles exhibit no extrapolar electrotonus, I then compared muscle to hard steel and nerves to soft iron[1]. The middle tract of a steel rod, surrounded by a coil through which a current is passing, becomes magnetic, and remains so after the cessation of the current; but it is only by action at a distance that the magnetism spreads beyond the tract immediately involved. If the rod is composed of soft iron it is magnetized throughout its length, although with diminishing strength, from the coil to the ends; but after the cessation of the current the magnetism entirely disappears. In the same way muscles and nerves then seemed to me to behave differently in relation to the polarisation of their electromotive molecules. But I had theorised too soon. When in the winter of 1852–53 I returned with improved apparatus to the investigation of secondary electromotive actions in nerves and muscles, I found at once that nerves also possess positive internal polarisability or power of coercion (*Coercitivkraft*), in accordance with the comparison just made, only that their polarisability is more difficult to seize upon than that of muscles, for reasons that are easily understood.

From the great importance which this phenomenon appeared to have in relation to the theory of electrotonus, I have since

[1] Untersuchungen, vol. ii. part i. p. 326.

repeatedly taken up the investigation as my views and methods improved, and innumerable experiments on polarisation of nerves have been lying for years in my note-books.

Among other things I had already, in the years 1857 and 1858, completed a table which exhibited the secondary electromotive actions in nerves for a series of times of closure and current densities in both directions. The experiments were made with the nerve-multiplier, the two sciatic nerves of a frog laid together being used. A new pair of nerves was employed for each time of closure, and each current density in each direction. Pflüger, who was then in Berlin, had the great goodness to assist me in these experiments. The table for nerves suffered in the same way as that traced out for muscles two years before, from all the faults which were attached to my results before the discovery of unpolarisable electrodes, of physiological salt clay, of the method of compensation and of the aperiodic galvanometer, besides which the strength of the primary current was not regularly nor closely enough watched. In spite of this I am obliged to make use of the older table, as it has not yet been possible for me, as in the case of muscles, to replace it with one less faulty. As, however, the results of the older table of nerves resemble very much those of the new table of muscles, perhaps the evil is not so great. Indeed the graphic representation given in Figs. 5 and 6 of the polarisation-curves, drawn relatively to the times of closure and opening, apply nearly as well to nerves as to muscles. Current densities less than a certain amount only give negative polarisation. With greater current densities of from 5 to 50 Groves, and very short time of closure, purely positive polarisation appears. With a somewhat longer time of closure, which amounted to perhaps 0·2 second, the polarisation in nerves was already in opposite directions, that is to say, a positive deflection immediately succeeded a negative one. If the time of closure amounted to more than a second, the polarisation was purely negative. I obtained the strongest positive polarisation with a very short closure, from 25 to 30 Groves; as in the case of muscle, the force remained apparently below that of the current of the nerve at rest. The strongest negative action resulted, exactly as in muscle, from the passage of relatively weaker currents for a longer time. After 45′ five Groves, after 15′ seven Groves, after 5′ ten Groves swung the needle against the stop of the multiplier, that is, a stronger action was produced than by the nerve-current. Here also, as in muscle, the observ-

ation holds good, that the resulting polarisation, which is the difference between two component polarisations, is no measure of their strength, for this may be many times as great as the observed difference. For, obviously, the various kinds of phenomena of nerve-polarisation lead unavoidably to the assumption that in nerves as well as in muscles there are present at the same time two polarisations,—a positive polarisation which at once attains almost its full amount although it continues to increase slowly and is very persistent, and a negative polarisation which increases with the time of closure, and rises more and more above the former, but disappears more quickly after the opening of the battery-circuit. Opening currents of the ordinary inductorium of an adequate strength produce purely positive polarisation.

In regard to the finer details of the phenomenon, the various maxima of polarisation-curves recognised in muscles, and the influence on the position of these maxima of current-density, time of closure, and time of opening, it is desirable to await further investigations, although even in this respect the old nerve-table, with all its incompleteness, has a certain resemblance to the new table of muscle. We know nothing as yet about the proportional strength and duration of polarisation in muscle and in nerve with an equal current-density, &c., and it would be very difficult to form a reliable conception of it.

14. Matteucci's Experiments on Nerve Polarisation.

I first gave an account of internal negative polarisation of nerves in 1856, in my paper upon this phenomenon in moist porous bodies generally[1]. In 1867 I again returned to it as a circumstance which is opposed to the constancy of currents in circuits containing nerves[2]. That nerves possess, in addition, internal positive polarisation, although perhaps in a manner only apparent to persons well informed on the subject[3], I have often pointed out when speaking of the secondary electromotive actions of electrical organs.

Although my papers on polarisation of electrolytes and moist porous bodies found their way into French and Italian journals[4],

[1] Monatsberichte etc., August 4, 1856, p. 457; Gesammelte Abhandlungen etc., vol. i. p. 19.

[2] Archiv für Anatomie, Physiologie, etc., 1867, p. 262; Gesammelte Abhandlungen etc., vol. ii. p. 192.

[3] Monatsberichte etc., 1858, p. 106; Untersuchungen am Zitteraal etc., p. 206.

[4] Il nuovo Cimento ec., vol. v. Maggio e Giugno, Pubbl. il 9 Luglio, 1857, p. 338; Annalès de Chimie et de Physique, 3me Série, 1860, vol. lviii. pp. 314, 318.

Matteucci in 1860, four years later than I and without mentioning me, described similar phenomena as if he had discovered them, and laid claim on the same occasion to the discovery of internal negative polarisation of nerves also.

Like me, he terms the actions 'secondary-electromotive.' His methods of investigation certainly do not resemble mine. He lays the two ends of a nerve first on the platinum electrode of a battery of from two to eight cells composed of zinc, carbon, and salt-water elements, passes the current through, from two seconds to three minutes, and then transfers the nerve to the multiplier pads. Negative polarisation is then found in the intrapolar tract, but positive in the two extrapolar tracts, and stronger in the one bordering on the kathode. These experiments were made not only with nerves of frogs, but also and by preference with those of warm-blooded animals, sheep, rabbits, and fowls. Negative polarisability was found to persist for several hours after the loss of vital properties. It was destroyed only by boiling temperature and compression. Matteucci attributes secondary electromotive action to the acids and alkalies set free at the platinum electrodes[1].

In a second communication, however, he alters his expressions in many ways in a manner peculiar to himself, without saying whether the first were mistaken or not. Now, the nerves were 'in most cases' not brought directly into contact with platinum electrodes, but passed through strips of woollen stuff steeped in spring water. The batteries were of 8 to 10 Groves, and the time of closure amounted to 25–30 minutes. He no longer speaks of polarisation of the extrapolar tracts, but now states that the part of the intrapolar tract adjoining the anode has a greater negative secondary electromotive force than that adjoining the kathode, and that the difference between them is greater when the current ascends than when it descends in the nerve. He professes to have convinced himself of this by opposing the two sections to one another in the same circuit. This kind of action he ascribes to contamination of the nerves with ions. Between the terminal portions of the nerves having an electro-chemical action of this kind, he seems to distinguish a middle portion, every point of which has a negative secondary electromotive action even after very short closure of the current[2].

[1] Comptes rendus etc., 27 Février, 1860, vol. l. p. 412; Archives des Sciences physiques et naturelles, Février, 1860, vol. vii. p. 173.

[2] Comptes rendus etc., vol. lii. 1861, 11 Février, p. 231; 13 Mai, p. 954.

In a third communication Matteucci returns to the extrapolar electrotonic currents, and there, as usual, repeats his statements on this subject many times with all kinds of variations[1], through which it is useless to follow him. On the polarisability of nerves, however, he founded his conception of extrapolar electrotonus currents as being escape-currents, which spread from the anode along the anelectrotonic tract externally, and reach the kathelectrotonic tract by the axis cylinder, along the outside of which they return to the kathode: all of this he imitated by a platinum wire covered by a moist coating. If such a wire is laid on a pair of electrodes, extrapolar diffusion of current occurs according to the law of electrotonus, but is absent when zinc wire covered by a coating steeped in sulphate of zinc has been employed. As is well known, this is the theory which has since been taken up by Hermann, to whose experiments on internal polarisation of nerves we now come.

15. Hermann's Researches on Nerve Polarisation.

In his paper of the year 1867, in which Hermann first advanced his necrosis hypothesis, he gave a philosophical[2] explanation of electrotonus in connection with this hypothesis, according to which a current opposed to the polarising current predominates in the intrapolar tract, which is comparable to Peltier's counter current in a thermopile through which an external current is passing. In this supposed coincidence Hermann saw a striking confirmation of his speculation and a new support of his view[3].

In my confutation I contented myself with exposing a flaw in the series of conclusions by which Hermann believed that he could connect his conception with the law of the conservation of energy[4]. I had reasons for not withdrawing the veil from the whole subject of the secondary electromotive actions of nerves with which only I and a few initiated people, such as Pflüger, were acquainted.

[1] Comptes rendus etc., 16 September, 1861, vol. liii. p. 503; 20 Avril, 1863, vol. lvi. p. 760; 22 Juillet, 1867, vol. lxv. pp. 131, 195; Annales de Chimie et de Physique, 3me Série, vol. lix. p. 385; Electro-Physiological Researches, Eleventh Series, Philosophical Transactions, etc., 1861, p. 363; Proceedings of the Royal Society, vol. xi. p. 384; Philosophical Magazine, etc., 4th Series, vol. xxiv, October, 1862, p. 311; Corso di Elettro-Fisiologia in sei Lezioni, date in Torino ec., Torino, 1861, p. 59.

[2] [The word used is 'naturphilosophisch,' which cannot be rendered in English. (Tr.)]

[3] Weitere Untersuchungen zur Physiologie der Muskeln und Nerven, Berlin, 1867, p. 40.

[4] Gesammelte Abhandlungen, vol. ii. p. 341.

In the general interest it would indeed have been better if I had at once told Hermann that positive polarisation prevailed in the intrapolar tract. The course of science in this direction would have been different, and perhaps more fruitful.

A year later Hermann brought forward his hypothesis anew, somewhat more carefully worked out; after having made use of some of the hints contained in my confutation; he this time made a point of supporting his electrotonus theory by experiments [1]. 'The battery consisted of from 2 to 6 very small Daniells; the nerve-current was always accurately compensated to zero before the passage of the current. The passage of the current lasted, on an average, for a minute.' Under these circumstances Hermann naturally succeeded in seeing nothing but negative polarisation in the intrapolar tract. As this result appeared to agree with his hypothesis that 'the splitting of the nerve-molecules is quickened by the kathode and retarded by the anode,' and as it appeared to contradict my molecular theory, he was satisfied to hold by it.

Hermann's experiments also embraced the extrapolar tracts with which Adolph Fick had occupied himself after Matteucci [2]. He and Hermann arrived finally at the same conclusion, though the latter really has the priority, inasmuch as Fick's first communications did not correctly represent the facts. These are in Hermann's words, 'Both the extrapolar tracts act for a short time after the current is broken, and both are directed away from the tract in which the current flows;' but the anelectrotonic after-current which is opposed to the polarising current is the stronger of the two [3].

In the meantime, Hermann allowed his hypothesis upon the different 'rapidity of splitting' (*Spaltungsgeschwindigkeit*) as the cause of the electrotonic current, to drop, and took up in its place Matteucci's above-mentioned explanation of the extrapolar electrotonic current by diffusion, the complete verification of which he made his chief task. His experiments on intrapolar negative polarisation served him now as a proof of Matteucci's hypothesis [4],

[1] Untersuchungen zur Physiologie der Muskeln und Nerven, Drittes Heft, Berlin, 1868, pp. 71 ff.

[2] Centralblatt für die medicinischen Wissenschaften, 1867, p. 436; Untersuchungen aus dem physiologischen Laboratorium der Züricher Hochschule, part i, Wien, 1869, p. 129.

[3] Handbuch der Physiologie, vol. ii. p. 164.

[4] Pflüger's Archiv für die Gesammte Physiologie, 1872, vol. vi. p. 357; Handbuch der Physiologie, vol. ii. pp. 164, 165.

as they had done formerly for his own. Matteucci's hypothesis is undeniably to be preferred, inasmuch as something may be made of it. It is a good discussable mode of conception, of which I am all the more ready to take account that the fundamental idea is my own. As early as in my researches in 1849 I considered expressly, and tested with all the apparatus which then existed, the possibility of explaining the extrapolar electrotonic current by the assumption then much in vogue, that the axis cylinder conducted, and the medullary sheath insulated. In that case a branch current would flow from the anode along the perineurium to the next cross section, along the axis cylinder to the section nearest to the anode, and back through the perineurium to the kathode. In this form, however, the hypothesis did not stand the test[1].

Whether it would do so in the form which Hermann gave it, on the ground of the inferior transverse conductivity of nerves discovered by him, I rather hesitate to believe on his word, and I have not yet had time to convince myself about it by experiments of my own. If I succeed in doing this I shall freely acknowledge it. In the meantime it is certain that the intrapolar tract not only possesses the negative polarisation which is rather physical, and on which the extrapolar currents may depend, but also that positive polarisation of a more physiological nature which my hypothesis requires. It is certain that even if the extrapolar electrotonic currents depend merely on diffusion of current, the nature of electrotonus as consisting in positive polarisation is not thereby affected. We should only be rid of the doubtful necessity of explaining its spread beyond the electrodes. It is further certain that while I discovered the positive polarisation of the intrapolar tract at a time when I possessed none of the apparatus of the present day, Hermann, who found this apparatus ready, has from 1867 till now overlooked the fact which is fundamental in the field upon which he appeared as a reformer. Finally, it is certain that all that he thought out regarding electrotonus, and which he propounded with so much confidence, is reduced to mere chaff in presence of this fact, and that the investigation of electrotonus in general must begin from this fact. Hermann stated that the comparison of a living nerve and one killed by exposure to steam, showed no apparent difference as a conductor in favour of the former, as must be the case if a current set free electromotive forces in the same direction as itself in the living nerve; and he regards

[1] *Loc. cit.* vol. ii. part i. pp. 229, 275–282, 347–350.

this experiment, which was moreover first suggested by me[1], though on account of theoretical difficulties it was not carried out, as an *experimentum crucis* against the molecular theory of electrotonus[2].

To Hermann's estimate of the electromotive force acting in a nerve whose dipolar molecules collectively turn their similar poles to the same side, I am the less able to object in principle that I explain the functions of the electrical organs by similar estimates[3]. That no force comparable with the calculated one appears in nerves has been vindicated by the assumption made by me already in the 'Untersuchungen,' that when the molecules are thrown out of the true direction in relation to the polarising current their rotation amounts only to a small angle, and not to 180°.[4]

The difficulty which Hermann's experiment offers disappears before the known facts of nerve polarisation. With a long time of closure, negative polarisation exceeds positive, and as boiling heat destroys both, the living nerve ought apparently to conduct worse than the dead one, not better, as Hermann expected. In order to find the living nerve a better conductor than the dead one the experiment must be made with a very short time of closure. Even then positive polarisation predominates over the negative only when the strength of the primary current is so considerable, that there is little hope of observing the slight excess of positive over negative polarisation when this is added to the primary force. There is, however, one experiment which might be explained in this sense. If a nerve closes the secondary circuit of an inductorium, the alternating currents of which would otherwise, according to well-known rules, compensate one another in the galvanometer, the quicker and shorter opening currents predominate, according to Fleischl. A single opening shock also passed through the nerve causes a stronger deflection than a closing shock[5]. Inasmuch as the opening shock is more exciting than the closing one, Hermann sees in this nothing more than a special case of his 'theory of polarisation

[1] Untersuchungen über thierische Elektricität, vol. ii. part i. p. 328.

[2] Untersuchungen zur Physiologie der Muskeln u. Nerven, part iii, 1868, p. 67; Pflüger's Archiv, 1872, vol. vi. p. 328; Die Ergebnisse neuerer Untersuchungen auf dem Gebiete der thierischen Elektricität, Sep. Abdr. aus der Vierteljahrschrift der naturforschenden Gesellschaft in Zürich, 1878, part i. p. 17; Handbuch der Physiologie, vol. ii. 1878, p. 172.

[3] Untersuchungen am Zitteraal, p. 275.

[4] Untersuchungen über thierische Elektricität, vol. ii. part i. p. 325.

[5] Sitzungsberichte der Wiener Akademie der Wissenschaften, 1878, part iii. vol. lxxvii. p. 159.

increment' (compare Sect. 19)[1]. After what I have just said about nerve polarisation, however, positive polarisation in Fleischl's experiment must exceed negative to a considerably greater degree in the case of the opening than in the case of the closing shock, and the possibility that this participated in the result is at least to be borne in mind.

If the negative polarisation does not spread beyond the poles (which I do not as yet consider proved), while positive polarisation does so (which I, for my own part, never regarded as demonstrated), we might perhaps believe that the extrapolar positive polarisation exceeded the similar intrapolar to some considerable extent. But I have no intention of entering now on a discussion of these obscure and complicated questions.

In so far as the extrapolar electrotonus currents outlast the opening of the polarising current, the intrapolarisation being however necessarily present during the closing of the battery, one sees that the distinction between the second and third of the different classes of electromotive phenomena in muscle and nerve referred to in Sect. 2, disappears, and it would be better to distinguish only two classes, that of the independent or primary, and that of the secondary phenomena, by including under the latter, without reference to the time of their appearance, all the phenomena an extraneous current generates as a current, and not merely as an irritant in muscle and nerve.

16. Tigerstedt's Experiments on Nerve Polarisation.

Last year Tigerstedt of Stockholm described some experiments on internal polarisation of nerves[2]. For certain reasons he led off the after-current through the same electrodes which had led in the polarising current. He used no stronger battery than three Meidingers. He regulated the time of closure with the hand, according to the metronome: the shortest amounted to 1″, the longest to 240″. The transmission time was determined by means of the Marcel Deprez's electromagnetic marker and varied between 0″·02 and 0″·04.

Tigerstedt also obtained only negative polarisation. He formulated his results as follows: '1. With a current up to three Meidinger cells the polarisation is almost directly proportional to the

[1] Pflüger's Archiv, 1879, vol. xix. p. 416.

[2] See Tigerstedt's paper on Internal Polarisation, p. 77 of this volume.

strength of the polarising current. 2. If the polarising current acts during an unequal length of time on the nerves under otherwise unaltered circumstances, the polarisation increases; it rises at first faster, and later more slowly, finally reaching its maximum extremely slowly. 3. If the polarising current is opened, the polarisation instantly reaches its highest amount, and after that sinks continuously. This decrease is at first very rapid, later on always slower, so that the polarisation persists a long time after the opening of the polarisation-current, and only approaches the zero point asymptotically.' Tigerstedt would certainly have met with the internal positive polarisation of nerves in his carefully-conducted experiments, if he had employed greater current densities and a shorter time of closure. As it was, however, he remained, like his predecessors, on the further side of the critical time of closure. Neither Hermann, Fick, nor Tigerstedt had a galvanometer in the battery circuit. I do not think that this was of any importance in their experiments, but I would caution any one from engaging in a series of experiments with strong currents and long times of closure without following this rule. (Sect. 6.)

17. On the Influence of the Direction of the Primary Current on the Secondary Electromotive Actions of Nerves.

It was the desire and hope of communicating something definite about the dependence of internal positive polarisation of nerves on the direction of the polarising current, that chiefly withheld me from publishing my investigations in their present condition. The remarkable fact that the greater strength of positive polarisation of muscle in the direction from the equator, in or near which the hilus is situated, towards the ends (Sect. 9), led me for a time to suppose that the intra-muscular nerves were concerned, and that they underwent a stronger positive polarisation in a centrifugal direction. This led me to the idea of experimenting as to how the motor and sensory roots of the spinal nerves would behave, in relation to internal polarisation.

Polarisation experiments on the roots are naturally made much more difficult by their shortness. The first requisite is to procure the largest possible frogs. In 1857 I measured a R. esculenta of 298 mm. and one of 305 mm. from the point of the nose to the longest toe. I succeeded, however, in applying four wedge-shaped

pads, covered with films of albumen, even to root-bundles of smaller animals. Though not absolutely necessary, it is very much to be desired that the experimenter in these researches should be able to give his undivided attention to the manipulation of the apparatus, and that he should be relieved of the trouble of preparation. Here again I remember, with heartfelt thanks, Pflüger's self-sacrificing assistance. During many a July afternoon in the tropical summer of 1857, while I kept everything in readiness at the nerve-multiplier, he prepared bundles, first of anterior and then of posterior roots, which, as it must be done as quickly as possible without pinching or displacing the roots, is not so easy as might perhaps be imagined.

In these experiments the battery consisted of only a few Groves; the time of closure amounted to about 0″·2. Any nerve-current present was compensated by means of a primitive arrangement, out of which the round compensator was subsequently developed[1]. The roots were placed, along with the four wedge-shaped pads, on a small support, the 'root carrier,' which could be rotated on a perpendicular axis. This allowed them to be reversed between the 'conducting vessels[2]' without risk of displacing them on the pads. The object of this was to obviate as much as possible the electrical inequalities of these vessels and any irreciprocity of conduction in the circuit (Sect. 10). The current was sent through the roots alternately, first in one direction and then in the other, the direction being changed every minute and a half. After every four experiments the roots were turned round. Such series as the following were thus obtained:—

THREE GROVES. TIME OF CLOSURE ABOUT 0″·2.

Motor Roots.

$$\left|\begin{matrix}-10^{\circ}\\+16^{\circ}\end{matrix}\right|\uparrow\left|\begin{matrix}-12\\+10{\cdot}5\end{matrix}\right|\downarrow\left|\begin{matrix}-11\\+16{\cdot}5\end{matrix}\right|\uparrow\left|\begin{matrix}-13\\+10\end{matrix}\right|\Big|.$$

Roots reversed.

$$\uparrow\left|\begin{matrix}-12\\+12{\cdot}5\end{matrix}\right|\downarrow\left|\begin{matrix}-11\\+11{\cdot}5\end{matrix}\right|\uparrow\left|\begin{matrix}-12\\+13\end{matrix}\right|\downarrow\left|\begin{matrix}-12\\+13\end{matrix}\right|.$$

Roots reversed.

$$\downarrow\left|\begin{matrix}-12\\+12\end{matrix}\right|\uparrow\left|\begin{matrix}-13\\+12{\cdot}5\end{matrix}\right|\downarrow\left|\begin{matrix}-14\\+12\end{matrix}\right|\uparrow\left|\begin{matrix}-12\\+12\end{matrix}\right|.$$

Sensory Roots.

$$\uparrow\left|\begin{matrix}-11\\+14\end{matrix}\right|\downarrow\left|\begin{matrix}-17\\+12{\cdot}5\end{matrix}\right|\uparrow\left|\begin{matrix}-11\\+13\end{matrix}\right|\downarrow\left|\begin{matrix}-17{\cdot}5\\+12\end{matrix}\right|.$$

[1] Gesammelte Abhandlungen, vol. i. pp. 176, 177.

[2] [Du Bois' 'Zuleitungsgefässe,' not so familiar now as formerly. ED.]

Roots reversed.

$$\left|\begin{matrix}-34\\+14\end{matrix}\right.\uparrow\left.\begin{matrix}-16\\+31\end{matrix}\right|\left.\begin{matrix}-41\\+12\end{matrix}\right.\uparrow\left.\begin{matrix}-19\\+32\end{matrix}\right\|.$$

Roots reversed.

$$\uparrow\left.\begin{matrix}-18\\+16\end{matrix}\right|\left.\begin{matrix}-28\\+16{\cdot}5\end{matrix}\right.\uparrow\left.\begin{matrix}-21\\+16{\cdot}5\end{matrix}\right|\left.\begin{matrix}-27\\+17\end{matrix}\right..$$

In order to judge of these figures correctly it must be remembered that the currents were still led off to the nerve multiplier through platinum in saline solution, in the old way. After a momentary current the returning needle would swing back over the zero point into the other quadrant, and here it would be perhaps carried beyond its deflection in the first quadrant in consequence of the charging of the platinum plates. The polarisation-current of nerves is not however comparable to an instantaneous current of this kind. Even the negative polarisation, although the more transitory of the two, sinks more or less gradually. The middle point of oscillation for the undamped needle is therefore temporarily transferred to the negative quadrant, as we will call it. In its backward swing the needle may indeed cross the zero point, but its positive deflection will not exceed its negative. If this should happen, we may conclude that action successively in opposite directions is present. Consequently where in the above table a larger positive number follows a smaller negative one, action in two directions occurred, that is to say, a negative after-current changed suddenly into a positive one, and the difference of the numbers gives an approximate measure for the comparative strength of the latter. Accordingly in both tables up to the mark || we have the expected result. The subsequent appearance of the opposite result reminds us of the reversal of the normal relation in the two halves of a regular muscle (Sect. 10). Almost without exception the series began normally in the roots, but frequently the reversal took place not later than the second or third momentary current. This was especially the case in the motor roots, as in the examples given the sensory roots exhibited the condition in question longer than the motor ones. If we consider that in these experiments both sides of the separated roots were brought into contact with white of egg and injured with electric shocks, one cannot avoid the impression that apparently, in spite of all imperfections, they render the thesis probable that,—In motor roots positive polarisation predominates in a descending direction, and in sensory roots in an ascending direction ; the direction in both cases being that of the physiological innervation wave. Certainly until more is known,

the same observation holds good as for the two halves of a muscle. For strong positive polarisation weak negative polarisation may be substituted in the thesis; thus we may say that in the motor roots the ascending negative polarisation predominates, in the sensory the descending. When discussing muscles I referred to reasons to be afterwards given, for taking the same view of them which I do of nerves.

Various circumstances, amongst others the arrival of the West African Malapterurus, compelled me to break off these experiments, and I was only able to resume them twenty-two years later, in the autumn of 1879. I was then furnished with all the apparatus invented during the interval, and this time kindly aided by Professor Gustav Fritsch, whose anatomical skill was the more welcome, that in a consignment of Hungarian frogs for which I was indebted to Professor Jendrássik of Pesth, we found no such giants as the waters of the Brandenburg Mark sometimes supplied formerly. This series of experiments also was not completed. It did not seem advisable to continue them during the winter, after the larger frogs had been used. After that I was under the necessity of devoting myself to the editing of Sachs' results. These new observations, however, yielded much that was of importance. First of all, I tested the behaviour of a mixed nerve-trunk by the method of experiment to which the roots were to be subjected. Here no definite difference was apparent between the actions observed when the current was ascending and when it was descending, as the following example shows:—

FIVE GROVES. TIME OF CLOSURE 0″·037.

Portion of the Sciatic Nerve between the Vertebral Column and the origin of the branches to the Muscles of the Thigh.

$$\downarrow\left\{\begin{matrix}-\ 5^{sc}\\+33^{sc}\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 2\\+36{\cdot}5\end{matrix}\right.\downarrow\left\{\begin{matrix}-\ 7\\+23\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 4\\+26\end{matrix}\right.\downarrow\left\{\begin{matrix}-\ 3\\+20\end{matrix}\right.\text{ etc.}$$

TIME OF CLOSURE 0″·031.—*Another similar portion.*

$$\downarrow\left\{\begin{matrix}-0{\cdot}5\\+23\end{matrix}\right.\uparrow\left\{\begin{matrix}-0{\cdot}5\\+15\end{matrix}\right.\downarrow\left\{\begin{matrix}-0{\cdot}5\\+21\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 1\\+17\end{matrix}\right.\downarrow\left\{\begin{matrix}-0{\cdot}5\\+17\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 1\\+17\end{matrix}\right.\downarrow\left\{\begin{matrix}-0{\cdot}5\\+21\end{matrix}\right.\text{ etc.}$$

Central portion of the nerve.

$$\uparrow\left.\begin{matrix}-\ 5\\+18\end{matrix}\right.\downarrow\left\{\begin{matrix}-\ 6\\+16\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 6\\+19{\cdot}5\end{matrix}\right.\downarrow\left\{\begin{matrix}-\ 8\\+15{\cdot}5\end{matrix}\right.\uparrow\left.\begin{matrix}-\ 5\\+18{\cdot}5\end{matrix}\right.\downarrow\left\{\begin{matrix}-10\\+\ 8\end{matrix}\right.\text{ etc.}$$

TIME OF CLOSURE 0″·076.

Lower portion with the peroneal and tibial nerves.

$$\downarrow\left\{\begin{matrix}-4\\+6\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 3\\+15\end{matrix}\right.\downarrow\left\{\begin{matrix}-\ 2\\+21{\cdot}5\end{matrix}\right.\uparrow\left\{\begin{matrix}-\ 3\\+14{\cdot}5\end{matrix}\right.\downarrow\left\{\begin{matrix}-2{\cdot}5\\+14\end{matrix}\right.\uparrow\left\{\begin{matrix}-2{\cdot}5\\+15\end{matrix}\right.\text{ etc.}$$

The actions are always in two directions, as is at once evident on the galvanometer, but the first negative deflection is sometimes limited to a scarcely perceptible jerk. The inequalities in the several series depend undoubtedly on the imperfection of the apparatus for regulating the times of closure and transmission. Taking together all the experiments I have up to this time made on mixed nerves, there appears a slight preponderance of ascending positive polarisation. In descending it seems to decrease, and indeed even to become reversed. However, the experiments are still too imperfect to permit of such a generalisation, at all events no discussion of the question whether this is connected with the proportion in which the two kinds of fibres are contained in the transverse section of the nerve, can be entered on. On comparison of the above series with those on sensory roots a striking difference appears in favour of the suggested law.

THREE GROVES. TIME OF CLOSURE 0″·037.

Sensory Roots.

$$\uparrow\left\{\begin{matrix}-2\\+4{\cdot}5\end{matrix}\right.\downarrow\left\{-7\right.\uparrow\left\{\begin{matrix}-1\\+9\end{matrix}\right.\downarrow-7\uparrow\left\{\begin{matrix}-2\\+6\end{matrix}\right.\downarrow-8\uparrow\left\{\begin{matrix}-1\\+9\end{matrix}\right..$$

Roots reversed.

$$\uparrow\left\{\begin{matrix}-5\\+13\end{matrix}\right.\downarrow\left\{\begin{matrix}-8\\+7\end{matrix}\right.\uparrow\left\{\begin{matrix}-5\\+13\end{matrix}\right.\downarrow\left\{\begin{matrix}-9\\+9\end{matrix}\right.\uparrow\left\{\begin{matrix}-6\\+11\end{matrix}\right.\downarrow\left\{\begin{matrix}-9\\+6\end{matrix}\right.\uparrow\left\{\begin{matrix}-5\\+13\end{matrix}\right..$$

It is remarkable, however, that the motor roots here again yielded a less favourable result.

FIVE GROVES. TIME OF CLOSURE 0″·015.

Motor Roots.

$$\downarrow\left\{\begin{matrix}-3\\+23\end{matrix}\right.\uparrow\left\{\begin{matrix}-2\\+17\end{matrix}\right.\downarrow\left\{\begin{matrix}-3\\+22\end{matrix}\right.\uparrow\left\{\begin{matrix}-2\\+20{\cdot}5\end{matrix}\right.\downarrow\left\{\begin{matrix}-3\\+17\end{matrix}\right.\uparrow\left\{\begin{matrix}-3\\+12\end{matrix}\right.\downarrow\left\{\begin{matrix}-4\\+16\end{matrix}\right.\Vert\uparrow\left\{\begin{matrix}-2{\cdot}5\\+17\end{matrix}\right.\downarrow\left\{\begin{matrix}-3{\cdot}8\\+18\end{matrix}\right..$$

Up to the mark ‖ the suggested law is pretty clearly expressed; but for the most part even to this extent such was not the case. I was no more successful with the nerves of the thigh.

If consequently the law cannot be considered to be demonstrated, on the other hand it is not yet determined that it does not hold. It is possible that a combination of current density and time of closure which I did not hit upon in my experiments is required, in order to demonstrate it on the motor roots. In order to make further progress we should require a consignment of bull-frogs (R. mugiens or Catesbyana) from North America. So far my

endeavours to procure them have been fruitless. The optic nerve of a large osseous fish ought to be an excellent object for the fibres which conduct centripetally, but this I have not yet found time to try. For fibres having a physiological centrifugal action there seems to be nothing better than the electric nerves of a Torpedo. I will not say anything of an abundance of other experiments which are here suggested. Even the experiments already communicated seem well deserving of the attention of physiologists. They present the first example of an electromotive difference between centrifugally and centripetally acting fibres. One might well in this case employ the expression of which Paul Erman made use with reference to the law of contraction: 'The mere suspicion of such a difference inspires awe[1].' One must therefore be all the more cautious. Even if the supposed law were demonstrated, it remains to be considered whether it must be regarded as an action of the physiological innervation wave, or a provision for facilitating its propagation in a definite direction. I once doubted its existence or even its possibility on theoretical grounds[2].

18. On the influence of various conditions on the Polarisation of Nerves.

Regarding the question of the conditions which influence the polarisability of nerves, I have scarcely any results which are methodically arranged. Matteucci already knew that nerves which have been exposed to boiling-heat do not any longer show a negative after-current (Sect. 14). If, however, the nerves are protected from drying and allowed gradually to die at a low temperature, they retain their secondary electromotive action for a long time but with decreasing strength. Even after one-and-twenty hours a trace of polarisation could be seen. For example, after this length of time, sensory roots which had lain undisturbed in the moist chamber gave with 2 Groves and 0″·031 time of closure:—

$$\uparrow \begin{cases} -10 \\ +3 \downarrow \end{cases} \Big| \begin{cases} -12 \uparrow \begin{cases} -11 \\ +3{\cdot}5 \downarrow \end{cases} \Big| \begin{cases} -14 \uparrow \begin{cases} -12 \\ +2 \end{cases} \end{cases}$$

The experiments belong to the same series as those last communicated. After twenty-seven hours, however, there followed only purely negative polarisation:—

$$\uparrow -9 \downarrow -9 \uparrow -9 \downarrow -9;$$

[1] Untersuchungen über thierische Elektricität, vol. i. p. 334.

[2] Ibid. vol. ii. part i. pp. 574, 575.

and there was no longer any difference between ascending and descending polarisation. After fifty-five and a-half hours there was still a trace of negative polarisation to be seen amounting to about one degree of the scale. When the negative polarisation alone remains, it is the same in both directions in the sensory roots. Consequently the difference which living roots exhibit with regard to polarisation by the ascending and descending currents, is to be attributed to positive polarisation; in both kinds of fibres, though less markedly in the motor fibres, the negative polarisation is as strong and the positive not weaker in the direction of the physiological wave of innervation than in the opposite direction. The question referred to in Sect. 10 has thus been decided as regards nerves as was anticipated, and the method I chose of representing it is justified.

Without having made the experiment on the two halves of the muscle, I do not doubt that it would yield a similar confirmation. We shall meet with another fact pointing in the same direction further on.

It would be interesting to make polarisation experiments with a bundle of nerve fibres without perineurium, such as one gets in the manner described by Harless[1].

19. Positive internal Polarisation in Nerves in conflict with Tetanus.

The idea suggested itself of transferring the experiment described in Sect. 12 as made on muscles to nerves, and to examine what influence the state of activity of nerves would have on their internal positive polarisation. Although this plan of research has been among my agenda since 1857, I have not succeeded in carrying it out. In the meantime another fact became known from a different source, which did not indeed directly answer the question here stated, but which made it possible to foresee the answer with some certainty. This was the fact discovered by Grünhagen, that the strength of a current passed through a nerve increases on tetanising the nerve. Grünhagen explains this increase by diminution of

[1] Moleculäre Vorgänge in der Nervensubstanz, ii. Abhandlung, Voruntersuchungen. Aus den Abhandlungen der K. bayer. Akademie, vol. viii. part ii. München, 1858, p. 538 ff.; cf. Charles E. Morgan, Archiv für Anatomie, Physiologie, etc. 1863, p. 340; Electro-Physiology and Therapeutics, etc., New York, 1868, p. 464.

resistance in the nerve[1]. It gives a measure of the improvement of methods that Grünhagen obtained a result for which I had sought in vain in October 1844, although my arrangements were faultless according to the knowledge we then possessed[2].

Hermann, who several years later made an independent discovery of Grünhagen's facts, showed that it was not on account of diminished resistance, but of an electromotive force aroused in the intrapolar tract, which he calls the 'polarisation Increment[3].'

This is hardly the occasion for testing Hermann's theory of the phenomenon, for the positive polarisation of the intrapolar tract will render it necessary for him to make some changes in his conceptions. The fact in itself has for us this significance, that if the positive polarisation during the duration of the polarising current in a nerve is strengthened by tetanus, this will probably also be the case with the positive after-current. There would then exist between the secondary electromotive actions of muscles and those of nerves this difference, that the condition of activity weakens the positive after-current in muscles and strengthens it in nerves.

20. On the Secondary Electromotive Phenomena of Electrical Organs.

I have already given an account of the secondary electromotive phenomena in the electrical organs of the Malapterurus in my 'Experimentalkritik der Entladungshypothese[4].' What I have already said shows how I was led to these experiments. The agreement between the polarisation-currents of muscle and nerve and those of the electrical organs, which I pointed out in my lecture on the West African Malapterurus in January, 1858[5], is now recognised.

A strip of the fish cut in the direction of its length exhibits[6] a secondary electromotive action like muscle or nerve. With medium

[1] Henle's u. Pfeufer's Zeitschrift für rationelle Medicin. 3 series, 1869, vol. xxxvi. p. 140.

[2] Untersuchungen über thierische Elektricität, vol. ii. part i. 1849, p. 444.

[3] Pflüger's Archiv, 1872, vol. vi. p. 561; 1873, vol. vii. p. 323 ff.; 1874, vol. viii. p. 264; 1875, vol. x. p. 215; 1876, vol. xii. p. 151; 1879, vol. xix. p. 416; 1881, vol. xxiv. p. 246; Handbuch der Physiologie, vol. ii. 1878, p. 165; Die Ergebnisse neuerer Untersuchungen, etc., Sep. Abdr. aus der Züricher Vierteljahrsschrift, 1878, p. 32.

[4] Gesammelte Abhandlungen, vol. ii. p. 718.

[5] Monatsberichte, 1858, p. 106.

[6] [Here the Multiplier was the instrument used. Ed.]

density of current, or greater density but longer time of closure, negative action follows in both directions, though weaker in the direction of the shock. With greater current density and shorter time of closure positive action appears, but is stronger in the direction of the shock. As the shock in the electrical organ is directed from the head to the tail we may describe the polarising current in that direction as a descending one, and the one in the opposite direction as ascending. Thus a purely negative after-current often follows a momentary ascending current, though the descending one generates a strong positive after-current. The latter is distinguished by its longer duration from a shock of the organ, however induced. While the shock deflects the needle in the same way as a momentary volta-electric current, the positive after-current actually holds it pressed against the stop for some time. At the same time the primary current is also stronger in the direction of the shock than in the opposite direction. From the great electromotive force which the primary current must possess in order to obtain positive polarisation, the electromotive force of this polarisation is relatively considerable. As it will probably be a long time before any one finds an opportunity of making such experiments again, I will communicate a few particulars and a few numbers to show what magnitudes we have to do with.

I had already made polarisation experiments on the smallest of the three fishes, sent to me by Goodsir, and which were killed on the 23rd November, 1857, in which however the primary current had not been observed. But I convinced myself, by their means, of the agreement of the secondary electromotive behaviour of the organ with that of muscle and nerve. For further experiments I used strips of the organ of the largest specimen, which was 233 mm. long. On the morning of the 12th of January the animal was found dead, yet the organ still gave reflex shocks on irritation of the skin with a forceps, so that a frog's leg, the nerve of which was applied to the fish, contracted. As its death was unexpected, the necessary galvanometrical apparatus was unfortunately not at hand. The only available galvanometer had to be kept for the primary current. The nerve multiplier was employed for the secondary actions. It soon proved to be too sensitive; but after the experiment was begun with it, it could not be exchanged for another instrument without sacrificing the comparableness of the result[1]. Had I then known the astonishing tenacity of life which the organ

[1] Gesammelte Abhandlungen, vol. ii. p. 718.

possessed, and which I then discovered for the first time [1], I should not have allowed myself to be deterred from at least beginning a new series of experiments with the muscle multiplier. As I did not know whether each action we observed might not be the last, naturally nothing could be obtained but a rough general outline of the phenomena. Filling up a table systematically with double entries, such as I already possessed for muscle and nerve, was not to be thought of.

The strip separated from the organ with scissors was about 30mm. long and from 5 to 8mm. wide. The thickness of the organ might have been 5mm., so that supposing the conducting power to be the same, the strip possessed about the same resistance as our group of muscles. The plan of experiment was the same as for muscles, except that, as the organ did not twitch, the stretcher and the wedge-shaped pads for conducting the polarising current were unnecessary. To the two ends of the strip were generally applied ordinary pads soaked in a solution of sulphate of copper covered with a film of albumen [2]. The wedge-shaped pads for leading off the current were steeped in saline solution, and also covered with films of albumen, and were continuous with the ordinary old form of conducting vessels with platinum plates in saline solution. Lastly, the alternate closing of the primary and secondary currents, the isolation of both circuits from each other, the control of the time of closure and so on, were effected by means of the same apparatus which I still use for muscle and nerve. With the exception that the external surface of the skin was slightly positive in relation to all the other surfaces of a strip of the organ, there was no trace of electromotive action in the organ at rest [3].

The following tabular statement, coming after all the others, will be comprehensible without further explanation. The roman numbers are Groves, the times are the times of closure, $+90^{\circ}+x$ indicates that the needle was deflected until the stop was struck. The deflections of the galvanometer, with ascending and descending currents, are strictly only comparable within the limits of one experiment, as the distance of the bobbin was often altered to make the reading of the deflection easier.

[1] Cf. Untersuchungen am Zitteraal, p. 188.

[2] It is stated in the Experimentalkritik, through an oversight, that the conducting pads were also wedge-shaped pads (*loc. cit.* p. 717).

[3] *Loc. cit.* p. 718; Untersuchungen am Zitteraal, p. 172.

		X.	XX.	XXX.		
				Fresh.	*Tired.*	*Exhausted.*
0″·2	↑S	−90°	−90	− 90	−90	−90
	P	15sc	25	118	44	57
	S	−90°	−90	+90+x	+70	−50
	↓P	15.	25	132	44	52
10″	↑S	—	−90			
	P	—	80·5 (steady deflection)			
	S	—	−90			
	↓P	—	81 (steady deflection)			
20″	↑S	−90				
	P	—				
	S	−90				
	↓P	—				

It is seen that the liminal strength for the appearance of positive polarisation is very high, between 20 and 30 Groves, and the primary descending current appears stronger than the ascending one in the proportion of 112 : 100. The table also shows that in the same strip, in proportion as its conducting power is exhausted after repeated experiments, positive polarisation recedes and negative reappears. In the same proportion the difference in the strength of the ascending and descending polarising current disappears.

The polarisability of the organ is reduced still more quickly and completely to a mere trace, by boiling temperature, which at the same time, as in muscle, lowers the resistance of the organ in a remarkable degree, as, e.g., in an experiment not specially directed to the observation of polarisation, in the proportion of 100 : 42.

		XXX.	
		Fresh.	*Boiled.*
0″·2	↑S	−90° (bis)	−24; −20
	P	45; 48sc	176; 176
	S	+90+x (bis)	−34; −26·5
	↓P	61; 80	186; 186

As stronger negative polarisation followed immediately, the greater strength of the descending primary current in the boiled piece had nothing to do with the preponderance which is observed in the same direction in fresh pieces, but for some reason there was a disturbance of reciprocity (see Sect. 10). That this preponderance

arises from positive polarisation, and that the preponderance of this polarisation in the direction of the shock is not merely accidental, follows further from the fact that when the current passes transversely nothing of the kind is observed.

Strip from the back cut transversely. 20 Groves.

		$l \leftarrow r$	$l \rightarrow r$
0″·2	S	+90°	+90
	P	76sc	76
10″	S	−90	−90
	P	92; 104	98

r, *l* indicate right and left. Through the thickness of the organ from the outer skin to the internal fascia 40 Groves with 0″·2 time of closure only produced 25° in both directions. The so-called *Hautschwarte* produced with 30 Groves and the same time of closure, only −2° in both directions.

From a piece of the organ I removed the skin and fascia; it continued to give secondary actions, though in a somewhat irregular manner, which was not surprising considering that it had lost all regularity of structure. No secondary electromotive action could be elicited from the fin, either with 30 Groves and a time of closure of 0·″2, or with 30 Groves and 20″, or with 20 Groves and 15″. Certainly this was the day after that on which the fish was found dead; but this would not account for the inactivity of the fin, if it were polarisable like the electrical organ, seeing that the latter still showed vigorous electromotive action. In fact, when kept in a damp chamber at a temperature of little over 0°C. the organ retained, like a dying nerve (Sect. 18), a small quantity of polarisability for an astonishingly long time, as is shown in the following table, in which the primary action is recorded only exceptionally, as a second observer was not always at hand.

XXX.

Jan.		13,	14,	15,	16,	17,	18, 1858.
↑ 0·2″	S	−90°	−90 + x	—	−90	−45	−8
	P	—	—	—	—	—	41sc
	S	+90	+60	—	−14 +48	−6 +12	−3 +6
↓	P	—	—	—	—	—	38

A strip perpendicular to the lateral line gave, with a current passed transversely through it on the 16th of Jan., −55° in one direction, and in the other −59°.

Thus on the sixth day after the death of the fish traces of polarisation were still present, according to the same law as for fresh organs. They finally disappeared with the properties of life, the

organ beginning to emit a peculiar stale odour. From a given moment the actions generated by the descending current are in two opposite directions. This is important, as it teaches that also in the electrical organ these actions are the algebraic sums of two polarisations, a negative more transitory polarisation, and a positive which subsides more slowly.

At my suggestion, the late Dr. Sachs began some experiments in Venezuela on the polarisability of the Gymnotus, the results of which I have already published so fully from his note book, as well as discussed in the 'Untersuchungen am Zitteraal,' that I have nothing to add to what has there been said[1]. I there showed that these results may be satisfactorily deduced on the supposition that in the organ of the Gymnotus, as well as in that of the Malapterurus, two polarisations exist together, a positive and a negative, of which the algebraic sum presents itself to observation; and that there also, the positive polarisation curve drawn relatively to the time of opening is the less abrupt, while the negative is the more abrupt. If Dr. Sachs never saw purely positive deflections, this is explained only too certainly by a defect in his outfit and instructions, for which I myself am to blame. He possessed only twenty small Groves, of which three arrived broken, an accident on which I should have calculated. Then I had not sufficiently impressed upon him, because it had not been enough brought home to myself, that he should use the smallest animals for these experiments and should cut the thinnest possible strips from the organ. Considering the exceptionally high liminal intensity which the electrical organ possesses for positive polarisation, and which perhaps lies still higher in the Gymnotus than in the Malapterurus, it is no wonder that Dr. Sachs with seventeen Groves and a piece of the organ of 6–7 cm. transverse section, obtained no purely positive deflections.

In the meantime, the discussion of Dr. Sachs' 'empirically resulting' curves supplied in some degree the lack of direct observation, as it left no reasonable doubt that both polarisations also co-exist in the organ of the Gymnotus. Dr. Sachs also convinced himself that boiling heat destroyed the polarisability of the organ. Thus everything appears to take the same course as in the Malapterurus. Unfortunately, however, there is an important difference between my experiments and Dr. Sachs' on another point. According to him, in the organ of the Gymnotus negative polarisation

[1] *Loc. cit.* pp. 205–221. The curves in Table II. of the work are, as will be easily recognised, in our present mode of expression, polarisation curves drawn relatively to the time of opening.

is stronger in the direction of the shock, while in the organ of the Malapterurus positive polarisation is the stronger. The difference as regards the relation between the nerve-ending and the direction of the shock in the two fishes might be referred to in explanation[1]. But in my work on Gymnotus[2] I explained the reasons why I did not consider Dr. Sachs' proof sufficient for his statement. Dr. Sachs had evidently no idea of the complete opposition to me into which he fell, and he contented himself with a single series of experiments on this difficult subject, during which he did not once observe the primary current and therefore was satisfied without guarding against irreciprocity of conduction. Under these circumstances, I must consider the question to be still an open one, which polarisation is the strongest in the organ of the Gymnotus in the direction of the shock; whether the positive, as in the organ of the Malapterurus, or the negative, as Dr. Sachs asserts.

Nothing is known as yet about the polarisability of the organ of the Torpedo, except that I discovered an experiment of Configliachi's of the year 1805 in which it appears that several organs of Torpedos laid upon each other were charged like a Ritter's secondary battery[3], i.e. were polarised negatively.

It is unnecessary to say that in the secondary electromotive actions of the electrical organs we have to do with the sum of the actions of the individual electrical plates. The view might be taken that on polarising the organ only the electrical nerves of the organ were the seat of polarisation. In the Malapterurus, however, the mass of these nerves is so small in proportion to that of the electrical structures, that this idea appears to be quite untenable.

I have already repeatedly treated of the teleology of the polarisation of the electrical organ—that is to say, of the part it possibly plays in the mechanism of the shock[4].

21. Theoretical. Closing Remarks.

The sum of the observations I have communicated, proves that muscles, nerves, and electrical organs are polarisable according to a common law, up to this time only observed in themselves. In addition to internal negative polarisation, which though at first sight indistinguishable from that of other moist porous bodies, yet is

[1] Cf. Gesammelte Abhandlungen, vol. ii. p. 618.
[2] *Loc. cit.* pp. 218, 219.
[3] Gesammelte Abhandlungen, vol. ii. p. 719, Anm.
[4] Gesammelte Abhandlungen, p. 722; Untersuchungen am Zitteraal, p. 220.

intimately connected with their vital properties, they are also capable of internal positive polarisation, which has never been observed elsewhere; and in all three, the positive polarisation appears more persistent, the negative more transitory, whence actions in two opposite directions, first negative and then positive, arise. It must however be remembered that I did not experiment with many nor the most important objects, such as glands, to see if they might perhaps show positive polarisation with greater current density and shorter time of closure.

My investigation of secondary electromotive actions is still in quite an unfinished condition, in which I am not in the habit of publishing results. I hardly think, however, I could have obtained the desired completeness by continuing to work at it longer without publication. Any one who has followed the preceding exposition must perceive that he has before him an overpowering mass of new facts and relations, so that although the best points of view may have been opened out and the right methods indicated, the exhaustive treatment of the subject would still require the lifetime of a new observer.

If, however, positive internal polarisation should be found in other moist porous bodies, that of muscles, nerves, and electrical organs will still remain distinguished by its peculiar relation to the vital activity of the structures. In regular 'monomeric[1]' muscles positive polarisation in the direction from the equator to the two ends is stronger than in the opposite direction. Unfortunately, in order to draw conclusions on substantial bases from this fact, accurate knowledge of the distribution of the nerve-endings in these muscles is wanting. I will not take up the question again as I have already discussed it[2], but will content myself with the remark that it is much the same whether each muscle fibre, as W. Krause states, receives its innervation only at a single point, or as Kühne says[3], at

[1] Gesammelte Abhandlungen, vol. ii. p. 570.

[2] Ibid. pp. 568 ff.

[3] I am not quite sure what Kühne's later views are on this point. He now discards, as based on imperfect examination, his statement that there are six or eight nerve-endings in the fibres of the sartorius (Über die peripherischen Endorgane der motorischen Nerven, Leipsig, 1862, 4°. Plate iii. Fig. xiv. F), and, as a proof of the innervation of muscular fibre at several points, he figures single nerve-endings of amphibia in which the nerve-fibre divides into several parallel terminal branches, which however in his theory form together only one point of innervation (Untersuchungen aus dem physiologischen Institute der Universität Heidelberg. Sonderabdruck, Heidelberg, 1879, pp. 115, 129; Untersuchungen am Zitteraal, pp. 416, 417). It is hard to see what this has to do with the question whether each muscular fibre receives its nervous supply at several points distinct from one another to the naked eye, or only at a single point.

several points, for on the whole a contraction wave will always run from the middle of the muscle to its ends. In the sensory, and less certainly in the motor nerve-fibres, positive polarisation predominates in the direction of physiological innervation. In the electrical plates of the Malapterurus it predominates in the direction of the shock.

Here it may be remarked, by the way, that there is no doubt that the positive polarisation is the stronger, and not that the negative is the weaker. If the polarising current density is but small, the negative polarisation which is then alone present appears equal in both directions. So also when exposure to a boiling temperature has left, instead of both kinds of polarisation, only a small residue of negative polarisation in the organ, this is the same in both directions just as it is in dying sensory roots. As it may therefore be considered proved that in electrical plates and in nerve roots it is the positive polarisation which becomes stronger in one direction, not the negative which recedes, we confidently apply the same explanation by analogy, to the behaviour of both polarisations in the upper and under halves of regular monomeric muscles, notwithstanding that a direct proof for this explanation is still lacking. In all three structures then—muscles, nerves, and electrical plates—positive polarisation appears more strongly in the direction in which the physiological process belonging to them—whether contraction-wave, innervation-wave, or electrical shock—is propagated in them. This view, if further verified, cannot be considered unimportant. For the possibility already discussed (Sect. 18), that the preponderance of ascending positive polarisation in the sensory roots may be only an action of the physiological innervation-wave which is frequently propagated in this direction, is rendered improbable by the necessity which it involves of attributing the same action to three perfectly different occurrences, the contraction-wave, the innervation-wave, and the electric shock.

In the endeavour to picture to oneself what takes place in each of these three structures during polarisation, one is naturally inclined to rank the negative polarisation in them with the internal polarisation of moist porous bodies. The idea at once suggests itself of connecting the destruction of the internal polarisability of muscles and of the electrical organ by boiling temperature, with the diminished resistance of the 'interstitial fluid[1]', and to connect its

[1] 'Binnenflüssigkeit.' This is the name which Munk has proposed for the interstitial fluid of moist porous bodies, so far as they indicate secondary resistance; it may also be applied to them as objects of polarisation (Archiv für Anatomie, Physiologie, etc., 1873, p. 254).

gradual disappearance in the process of dying with the acidification, which, according to Ranke, lowers the resistance of muscle 2–4 times more than boiling temperature[1]. In agreement with this also is the observation of Ranke that the connective tissues which do not lose their internal polarisability by exposure to a boiling temperature (Sect. 11) undergo through it no diminution of their resistance. On the other hand, it is not clear why a boiling temperature is more injurious to polarisability than death is, since the latter reduces the resistance considerably more than boiling temperature; and the general question is whether such a small reduction in the resistance of the interstitial fluid as occurs on boiling the muscle, is capable of an action for which the conducting capacity of vinegar, ammonia, sulphate of copper and zinc solution is insufficient in other porous bodies, such as blotting-paper[2].

Ranke places nerves among the tissues, the resistance of which undergoes no alteration through boiling heat or death; this creates further difficulties[3]. In analogy with the white matter of the brain, it may be inferred that the nerve-trunks are rendered acid by a boiling temperature[4]. This would explain the destruction of internal polarisability at a boiling temperature, were it possible to understand why the resistance of boiled nerves does not diminish, and why dying nerves which do not become acid, lose their polarisability[5].

There is still another consideration in opposition to the view that negative polarisation of muscle and nerve is a simple physical occurrence like the internal polarisation of wood, leather, etc. The dependence of this negative polarisation on current density and time of closure agrees well at first sight with such a view. Negative polarisation seems to increase at first to some extent proportionally to the product of these variables. It then slowly approaches a limit. This is exactly the behaviour to which we are accustomed in polarisation-currents generally, and which is easily explained by the nature of polarisation. In muscles, however, and if I may trust my old observations, also in nerves, a maximum of negative polarisation makes its appearance with an increasing time of closure.

[1] Regarding the acidification of boiled and dying electrical organs, see the Gesammelte Abhandlungen, vol. ii. p. 646; Untersuchungen am Zitteraal, p. 70.

[2] Tetanus; Eine physiologische Studie, Leipzig, 1865, pp. 35 ff.

[3] Gesammelte Abhandlungen, vol. i. pp. 25, 26; vol. ii. p. 190.

[4] *Loc. cit.* pp. 33, 38.

[5] Gscheidlen in Pflüger's Archiv, 1874, vol. viii. p. 171. Oddly enough, there seem to be no experiments on the reaction of boiled nerve-trunks themselves. Comp. Hermann in his Handbook, p. 139.

This does not agree well with the idea that we have here to do with ordinary internal polarisation. That this maximum points to an increase of positive polarisation which appears at this time is the more difficult to admit, inasmuch as the maximum appears rather to be coincident with the destruction of polarisability by prolonged action of very strong currents (Sect. 11).

The help which the comparison of the negative polarisation of muscles, nerves, and electrical organs with ordinary internal polarisation gives in explaining it, is entirely wanting as regards positive polarisation. If negative polarisation could be identified with ordinary internal polarisation, it would be covered by the physical process in the hypothetical septa referred to in Sect. 3. Of the occurrence of negative and positive polarisation in the same electrodes there is only one example observed by me, viz. that of iron, and zinc containing iron in a solution of zinc sulphate[1]. Although this double polarisation depends on the time of closing and opening, in the same way as that with which we are now occupied, we can scarcely have recourse to it for an explanation. In order to refer the polarisation of muscles and nerves and electrical organs to known physical facts, it is therefore necessary to assume another frequently recurring discontinuity in the direction of the current, which, like the surfaces of certain electrolytes, would be the seat of a positive polarisation[2]. If such a discontinuity could be assumed in muscle, or even in nerve, it would still be entirely wanting in the electrical plates of the malapterurus. It would also be very hazardous to suppose the existence in three such different structures of any such alternation of materials as could produce secondary electromotive actions. Besides, the positive polarisation in the electrical organs is much too strong to be thus explained.

In addition to this there is the peculiar manner in which positive polarisation depends on current density, and on times of closure or opening. Without reference to the maximum in prolonged time of closure, the dependence of negative polarisation on these conditions is at all events similar in form to that of the internal polarisation of moist porous bodies. This is not the case with positive polarisation, in respect of which there is a liminal intensity of the current density, below which it does not appear at all. It then appears suddenly with a force which increases indeed with current density, but slightly if at all with the time of closure. The limen lies higher for the electrical

[1] Gesammelte Abhandlungen, vol. i. pp. 57-60.
[2] Ibid. vol. i. p. 6.

plate than for muscle and nerve. While negative polarisation quickly disappears with increasing time of opening, like the internal polarisation of porous bodies, positive polarisation shows a persistence which points to another kind of mechanism. It should not however remain unnoticed that negative polarisation also persists a long time at the junctions of saturated solution of sulphate of zinc, and physiological solution of salt [1].

Although, then, traces of positive polarisation can be detected for a long time in nerves and electrical plates which are dying at a low temperature, it is more dependent on the vitality of the structures than negative polarisation. Boiling heat destroys it at once and absolutely, although still leaving a remnant of negative polarisation; and the destructive action of strong currents on polarisability in general attacks principally positive polarisation. In addition to this, the importance and bearing of the phenomenon may be inferred from what has already been said as to its relation to the direction of contraction, to that of innervation, and to that of the shock in electrical fishes, as well as to its not less important relation to the state of activity of the tissue.

I do not think that any one trained in physics and who keeps these facts before his eyes in their totality and in an unprejudiced manner, will arrive at any other conclusion to-day than that to which I was compelled to come many years ago. It is the conclusion not that in positively polarisable structures electromotive forces having the same direction as the primary current are generated, but that the conducting molecules (*Träger*) of electromotive forces already existing take the direction of the primary current. If to this it is added that in the natural condition of the structures the electromotive molecules are maintained by certain forces in a position, from which, although they can be displaced by the weakest currents, they can be removed permanently only by currents of a certain density, this simple and natural assumption reconciles the known liminal intensity of positive polarisation with the electrotonising properties even of the weakest currents. It is unnecessary to mention that the great persistence of positive polarisation agrees equally with this view.

As I became acquainted with positive polarisation of muscle shortly after the publication of my 'Preliminary Sketch' (1843), and long before that of the first volume of the 'Untersuchungen' (1848), it is easy to see how I arrived at the conception of the

[1] Gesammelte Abhandlungen, vol. ii. p. 190.

electromotive phenomena of muscle and nerve expressed in that work. The generalisation by which I concluded from the positive polarisation of muscles that there was also polarisation of the intrapolar nerve-tract, had perhaps something of youthful rashness in it, but nature proved me to be right when a few years later, I discovered in the positive after-current of nerves an indication of the prevalence of positive polarisation during the primary current. In so far as no other reasonable explanation of positive polarisation could be given, excepting that which regards it as due to the directing of already existing forces, the evidence obtained of this polarisation is at the same time serviceable in another way. In my eyes it afforded and will continue to afford proof of the presence of electromotive forces in uninjured nerves, a proof which, in the absence of a natural transverse section of a nerve, was otherwise lacking. The evidence of the existence of such forces in muscle obtained by carefully testing the natural transverse section of muscle, is also strengthened by it. In the same way I hoped to show the electromotive forces of muscles at rest in living men, the observation of which is rendered impossible by cutaneous currents, by parelectronomy, and by derivation through the skin. I had this in my mind in the experiments described in Sections 11 and 12, and in this sense the secondary electromotive phenomena should form the conclusion of the eighth chapter of the 'Untersuchungen' which treats 'of the muscle-current and its motor phenomena in living uninjured animals[1].'

Furthermore, as I now saw the possibility of explaining the electromotive forces of the shock in electrical organs by the physiological polarisation of molecules (*Trägern*); as I was fortunate enough here also to prove the existence of positive polarisation on the largest scale and in undoubted connection with the shock of the organ; lastly, as Delle Chiaie's and Babuchin's statement regarding the preformation of electrical elements in the organs of electrical fishes leaves no doubt of a pile-like strengthening of the shock in the plate,—therefore it need occasion no surprise that I still believe myself on the right road, and that for the present I contemplate with calmness the polemic which Hermann has directed against my views for sixteen years, and which has hitherto been more fruitful in technical expressions than in new facts. Repeatedly, and from two quite different hypothetical bases,

[1] *Loc. cit.*, vol. i. p. 240; vol. ii. part i. p. 331; part ii. pp. 1, 377.

Hermann has demonstrated that in the intrapolar tract a polarisation-current *opposite* to the polarising current must prevail (Sect. 15). I am curious to see to what auxiliary hypothesis he will have recourse for an explanation of the actual polarisation-current which is in the *same* direction.

These 'directable' carriers of electromotive forces in muscles, nerves, and electrical organs, referred to above as molecules, I have, as is well known, called electromotive molecules; and without in the first instance saying anything about their nature, I represented them diagrammatically in the simplest manner [1]. The discovery of inclination-currents (*Neigungströme*) placed me later in a position to state something definite about the arrangement of pre-existing electromotive forces in muscles. In the place of spheres of which one half was electro-positive, the other electro-negative, there came electromotive discs (*Flächenelemente*) [2], while at the same time I completed the representation which had remained unfinished in the 'Untersuchungen,' by representing these elements as foci of chemical change something like that which constitutes tissue respiration.

I know the difficulties that stand in the way of these views as well as any one. Here the question is how to represent the directing of the electromotive molecules by the current. In order to make it clearer, I had referred to Grothuss' theory of electrolysis. Hermann erroneously imputed the idea to me that the current rotated the molecules electrodynamically, and he tried to deduce this rotation from Ampère's fundamental law by substituting for a molecule capable of being directed a current element capable of being rotated, and for the total current a thread of current passing through the middle of the element [3]. Later on Hermann remarked indeed that he was presenting me with a theory with which I was unacquainted, but notwithstanding he thinks himself justified in setting forth my electrotonus hypothesis in this form (calling it simply the 'electrodynamic hypothesis'), on the ground that Grothuss' view is not applicable to electromotive molecules separated by interstitial fluid [4].

I had good grounds for avoiding any electrodynamic theory of the sort. Hermann's view is quite inadequate. The problem of

[1] *Loc. cit.*, vol. ii. part i. p. 323.

[2] *Loc. cit.*, vol. ii. pp. 122, 291, 671, 672.

[3] Untersuchungen zur Physiologie der Muskeln und Nerven, part iii. p. 66. Berlin, 1866.

[4] Pflüger's Archiv, 1874, vol. viii. p. 268; Handbuch der Physiologie, 1878, pp. 171, 172.

determining the electrodynamic interaction between an electrical current and an electromotive molecule certainly raises several knotty points, nevertheless, so far as the electrodynamic forces are known with certainty, it may now be affirmed that no rotation of the molecule through these forces is possible.

So far as Grothuss' theory in its original form presupposes that atoms of oxygen and hydrogen form a kind of molecular chain in the conductors of the second class undergoing electro-chemical decomposition, this representation does not agree strictly with the polarisation of muscles, nerves, and electrical organs by the current. The explanation I gave in the 'Untersuchungen' even now seems me to sufficient to give to the theory of directable molecules as much plausibility as is usually attainable in dealing with molecular processes of this kind.

It has indeed since then received some support from the discovery of the anaphoric actions of the current by Jürgensen [1], and their explanation by Quincke [2]. If particles floating in a fluid and negatively electrified by contact with it, migrate to the anode before our eyes, the conclusion does not seem too venturous that a molecule of which one half is electropositive, the other half electronegative, not displaceable but capable of rotating freely, would turn its positive pole to the kathode and its negative to the anode.

But I attach little importance to such speculations. It is quite sufficient for me to know that in muscles, nerves, and electrical organs, carriers of electromotive forces exist which the current somehow directs, which are in relation to the vital activity of these structures, and in electrical organs serve to explain their enigmatical action.

In the face of the profusion of questions regarding facts which are here awaiting an answer, I consider it lost labour to indulge in further conjectures. One can scarcely hope to penetrate more deeply into the molecular mechanism of electromotive tissues until the region of secondary electromotive phenomena has been explored in every direction.

[1] Archiv für Anatomie, Physiologie, etc., 1860, p. 673.

[2] Poggendorff's Annalen der Physik und Chemie, 1861, vol. cxiii. p. 565.

VII.

ON

DU BOIS-REYMOND'S RESEARCHES

ON SECONDARY ELECTROMOTIVE PHENOMENA OF MUSCLE.

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Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Vienna,
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VII.

In my twelfth communication[1] I mentioned du Bois-Reymond's treatise on 'Secondary Electromotive Phenomena in Muscle, Nerve, and in Electrical Organs,' in which he arrives at deductions directly contradicted by facts which I have established. Du Bois-Reymond concludes from his researches that when an electrical current flows through a muscle, it polarises the whole of the region through which it flows. If this is so, every part of the intrapolar region lying between the galvanometer electrodes should, on breaking the circuit, give an after- or polarisation-current, which, according to the density and duration of the primary current, now opposes, now reinforces it. Equal lengths of the intrapolar region should give equal polarisation-currents, provided the sectional area be the same throughout, so that it would be of no importance from what portion of the intrapolar region the polarisation-current was led off, so long as the length of that portion remained the same.

Provided the resistance in the galvanometer-circuit is sufficient, the current of polarisation should be correspondingly stronger if the leading off electrodes include a longer tract than if they include a shorter tract, on account of the greater number of electromotive parts between the galvanometer electrodes, and therefore strongest when the whole intrapolar tract is interposed. In this respect the positive or negative polarisation-currents would be quite analogous to the negative polarisation-currents of a charcoal cylinder steeped in weak sulphuric acid, on which account, moreover, du Bois-Reymond assumes an 'internal polarisation' for the whole of the intrapolar tract.

[1] Über Veränderungen des elektromotorischen Verhalten der Muskeln im Folge elektrischer Reizung. Sitzungsberichte, vol. lxxxvii. p. 415.

In contradiction to this, I have arrived at the conclusion that the polarisation-currents in a muscle consequent on breaking the primary or stimulating current, result solely from alterations which the latter undergoes at any point of the contractile substance of the muscle-fibres at which it enters or leaves that substance; in short, at the anodes and kathodes. So long as the current flows in a direction which is mathematically parallel with the muscle-fibres, in all probability it does not polarise them at all; at least there is not a single recorded observation which would lead one to such a conclusion. If polarisation of the muscle-substance occurred in the intrapolar tract (in the strict sense of the term), in any case it would be so trifling that it might be provisionally quite neglected in comparison with the polarisation-currents which accompany changes at the anode and kathode. Without prejudging in any way the essential nature of these changes, they may be regarded as a polarisation which has an analogy with external polarisation, but certainly not with internal.

This holds at least for negative polarisation, whilst positive, resting as it does on excitation of the living substance, does not admit of comparison with physical polarisation.

The changes which occur at the anodes of the contractile substance in consequence of stimulation, I call anodic polarisation, those which occur at the kathodes, kathodic polarisation of those spots. In a muscle-fibre through which a current is passing in a longitudinal direction, only a portion where there are no anodes nor kathodes is to be understood as an intrapolar tract. But, whereas in a 'monomerous' muscle, the fibres of which are parallel and through which a current is passing, the anodic or kathodic spots are for the most part aggregated in the region where the current enters or leaves the whole muscle, the tract between these two spots can with approximate accuracy be termed the intrapolar tract.

At the same time it must not be forgotten that in point of fact, on grounds which I have already discussed, there are always individual anodic and kathodic spots within this tract even when no muscle-fibre terminates in it. Finally, it must not be forgotten that there are other tissues in a muscle besides the muscle-fibres, which possibly might be appreciably polarised.

According to my interpretation, the positive polarisation-current consequent on changes at anodic spots of the contractile substance is a so-called action-current, and is generated by a break-excitation

originating in the neighbourhood of the anode—an action-current indeed which behaves in a manner essentially different from the action-currents consequent on instantaneous stimulations. Nevertheless, I will provisionally speak of this break action-current as a polarisation-current.

The facts contained in the preceding communication gave sufficient evidence that the internal polarisation adopted by du Bois-Reymond was not the actual cause of the secondary electromotive phenomena observed by him; yet I feel it my duty to give a still more thorough refutation of his interpretation of those phenomena.

I.

In his researches, du Bois-Reymond made use of two muscles at the same time, i. e. the *rectus internus major* (Ecker), which Cuvier calls *adductor magnus* and du Bois-Reymond *gracilis*, and the semimembranosus (Cuvier, Ecker, du Bois-Reymond).

The first tapers to a thin tendon at both ends, and is a tolerably symmetrical muscle. A tendinous intersection, (*inscriptio tendinea*,) however, runs obliquely through the middle third, which completely divides the muscle into an upper and a lower portion.

The greater portion of the semimembranosus is likewise traversed by an oblique tendinous intersection, hence it only partly consists of long fibres. Besides this it is very unsymmetrical, rising by a broad tendon from the pelvis, and tapering from above downwards, at first gradually, afterwards rather rapidly, to end in a thin tendon. The intersections of both muscles were fully described and depicted by du Bois-Reymond in a former research [1]. He noticed moreover 'that the semimembranosus in a portion of its length from below upwards receives fresh accessions of fibres, which arise from both sides of a strip of tendon projecting at its outer side.'

Both muscles were so prepared for the purpose of experiments on polarisation, as to remain attached to each other, and in addition to portions of the pelvis and tibia. By means of these bones they were extended on a 'muscle-frame' or stretcher and arranged as one single thick muscle.

'Close to the ivory plates of the stretcher, the wedge-shaped pads

[1] On negative variation of the muscle-current; Gesammelte Abh. vol. ii. p. 575.

of the polarising current were brought into contact with the muscle from the inner (femoral) side; between these, on the outer side, the electrodes were placed to lead off the polarisation-current. On account of the high resistance of the tendons, which would become heated and dried, it is impossible to lead the current to the muscle by means of ordinary pads applied to the fragments of bone outside the ivory plates; a method which otherwise would have had great advantages.' With reference to the last point, I may mention that du Bois-Reymond used up to as many as 50 Groves. I at first never went beyond 8 Daniells, for I only wished to stimulate the muscle, not seriously to injure it at the same time.

In order to understand the results of du Bois-Reymond's researches, it will next be necessary to indicate how the anodic and kathodic spots are distributed in the muscle.

The current from the stimulating anode as it enters the natural longitude of the muscle near its tendon cannot, as a rule, enter the contractile substance through the natural transverse section of the individual muscle-fibres; it must rather in its course from fibres in the neighbourhood of the electrode to fibres at a greater distance from it, pass through the first-named transversely or obliquely. Hence, the lines of current radiating from the electrode become parallel to the muscle-fibres only at some distance from their source. Every fibre through which a portion of current flows in a transverse direction has both anodic and kathodic spots. Moreover, as the double muscle taken as a whole tapers off at the upper and lower ends, a considerable number of its fibres terminate at varying distances from the commencement of the proper tendons. In the case of the semimembranosus there is in addition the circumstance above mentioned, that it has considerable accessions of fibres in the direction from below upwards.

If the current entered and left through the tendons, the whole tract of muscle in which fibres take origin or in which they terminate would have a corresponding number of anodic or kathodic spots, and one portion of the muscle would present an anodic tract, the other a kathodic, understanding thereby the tracts of muscle in which the anodic and kathodic spots are respectively aggregated. If the stimulating electrodes are applied to the longitudinal surface of the muscle but near the tendons, and yet in the tapering part of the muscle, the current would meet numerous muscle-fibres in its course, and would enter or leave them through their natural ends. More especially would this be the case, as

we have already shown, at the lower end of the semimembranosus.

The significance of the circumstance, that the greater portion of muscle-fibres in the neighbourhood of the anode are crossed by transversely or obliquely running lines of current, and hence that every such fibre has anodic spots of somewhat greater density of current on the side turned towards the stimulating electrodes, and kathodic spots of somewhat less density on the other side, we shall not discuss at length here, for in order to do so it would be necessary to go minutely into the so-called transverse polarisation of muscle. In any case, it is apparent from the above-described distribution of anodic and kathodic spots, that from the stimulating electrode which lies on the side of the muscle in the neighbourhood of the tendon, to the point where the muscle no longer sensibly increases or diminishes in thickness, anodic or kathodic spots must prevail as the case may be, and hence the whole tract must be regarded as anodic or kathodic.

Now, when the stimulating electrodes are in the neighbourhood of the tendons of the muscle, and the galvanometer electrodes lie near them, the galvanometer electrodes are within the region of the anodic and kathodic tract, and this is the case at the lower end of the pair of muscles on account of the unsymmetrical structure of the semimembranosus, even if the stimulating electrodes lie at some distance from the tendinous end.

Even if the muscles had no tendinous intersection, still there would be a polarisation-current in the galvanometer-circuit after every break of the stimulating current, because all the anodic and kathodic spots lying in the anodic and kathodic tracts are the seat of a change caused by the stimulating current, which change must have an electromotive action.

Du Bois-Reymond has not stated how far the galvanometer electrodes were from the stimulating electrodes, and these, as appears from the description, were very near the tendons of the pair of muscles. It is very probable that both galvanometer electrodes were within the limits of the anodic and kathodic tracts, and this may be assumed in any case of the lower electrode, because, as we have already stated, the semimembranosus receives new fibres very high up.

But even if the galvanometer electrodes were at such a distance from the stimulating electrodes that they were completely withdrawn from the limit of the anodic and kathodic tracts as above

defined, and that from the electromotive changes taking place in this region set up by the stimulating current no polarisation-current could flow into the galvanometer electrodes, yet the far more important polarisation occurring at the tendinous intersections would not be excluded.

For between the two galvanometer electrodes lies the tendinous septum, which severs the two muscles in such a way that each consists of two separate muscles lying one behind the other. In front of the intersection the current leaves the fibres of one of the separate muscles, and behind it, enters the fibres of the second separate muscle. On one side, therefore, of the intersection lie innumerable kathodic spots, on the other side as many anodic spots, and the former as well as the latter are the seat of polar changes. The change at the anodic spots gives rise to a polarisation-current, and that at the kathodic spots gives rise to a second such current. As was shown in the first communication, both currents, according to circumstances, flow sometimes in the same direction, sometimes in an opposite direction to the stimulating current. The polarisation-current entering the galvanometer-circuit, represents the sum, or the difference, in short, the algebraic sum of both currents, which would appear separate if either the whole of the anodic spots or the whole of the kathodic spots could be suddenly rendered inert at the tendinous intersection.

Hence du Bois-Reymond's researches prove nothing with regard to an 'internal polarisation,' that is to say, with regard to the fact that the stimulating current polarises the contractile substance in the proper intrapolar tract, where it runs within the contractile substance of all the fibres.

The polarisation-currents described by du Bois-Reymond were for the most part the result of polarisation taking place at the tendinous intersection, or the algebraic sums of the two polarisation-currents produced there.

Besides this, polarisations in the neighbourhood of the upper, and still more in that of the lower electrode, became more considerable the nearer the galvanometer electrodes were to the stimulating electrodes. Hence du Bois-Reymond observed the algebraic sum of four synchronous polarisation-currents.

Another special disadvantage in the experiments of du Bois-Reymond consists in the fact that the tendinous intersection of each of the muscles used by him runs in a very oblique direction to the axis of the muscle, and that the intersections of the two muscles

diverge from one another. The tract which extends from the upper end of one of the muscles to the lower end of the other is equal to about half the length of the muscles themselves. This whole tract was, so to speak, anodic and kathodic at the same time; and it would have been necessary to put the galvanometer electrodes on the end quarters of the muscles in order to escape it.

If this was done, however, they would get into the region of the anodic and kathodic tracts in the neighbourhood of the stimulating electrodes. Taking into consideration the fact that the direction and strength of the polarisation-currents produced by one stimulating current depend on its density at the individual anodic and kathodic spots, and that in every muscle there must be two break-stimulations, which affect sometimes a larger, sometimes a smaller muscle tract (see below), it is easy to see under what extraordinarily complex conditions du Bois-Reymond's experiments were conducted. On this ground, also, it is not possible to deduce the theoretical result of each experiment.

According to the propositions set forth in my last treatise some points appear explicable, viz. first, that very weak currents invariably only gave negative polarisation. This was inevitable, for such currents produce negative polarisation at the anode as well as at the kathode, hence in such cases the total result of the combined anodic and kathodic polarisations of du Bois-Reymond's preparation could only be a negative polarisation-current.

Again, it is clear why very strong currents of short duration only gave positive polarisation-currents. For such currents either affect the anode only, and always in the direction of positive polarisation, or in any case their positive anodic action is much stronger than their negative kathodic action; hence the combined result of the polarising actions can only be a positive one.

With very weak currents, as well as with strong ones of short duration, the relations are much simpler and more easily reviewed, because the persistent break-stimulation is then confined to those portions of the fibres immediately adjacent to the anodic spots. Stronger stimulating currents of longer duration, after the break, effect however a persistent stimulation spreading farther in the direction of the stimulating current. As a necessary consequence of this in du Bois-Reymond's preparation, the galvanometer electrode which was next the stimulating anode, came within the limits of the stimulated and therefore relatively negative muscle tract, when the break-excitations were strong. If the galvanometer electrodes

were at such a distance from the exciting ones as to be beyond the limits of the corresponding anodic and kathodic tracts, and the exciting currents were weak or of very short duration, the polarisation-currents produced at the intersection would be, in fact, the only ones which manifested themselves galvanometrically. But even when the exciting currents were stronger or more protracted, and persistent break-excitations were induced, a new factor must have come into play.

Every stimulation with persistent and stronger currents necessarily induces persistent break-excitation in two tracts of the muscle; in the first place, an excitation which, commencing in the region of the stimulating anode spreads more or less towards the centre of the muscle, and a second which starting from the tendinous intersection spreads more or less towards the stimulating kathode. These two concomitant persistent excitations must, as a rule, be of different strengths and extent, for the conditions under which the current enters the individual fibres of the muscle from the stimulating electrode applied laterally, are quite different from those under which it enters the natural cross sections of the fibres of the second half of the muscle from the tendinous intersection. It is at all events plain, that the relations of current density in the anodic spots of the individual fibres must be quite different in the one case from what they are in the other, and on these current densities depends essentially the break-excitation of each fibre.

Another equally complicating element I have hitherto only incidentally mentioned. Every polarisation-current is to be regarded as the algebraic sum of the individual amounts contributed by the muscle-fibres. Supposing, for example, the current entered the thin end of a muscle and passed thence to its thicker centre. The current would in this case decrease in density so long as there was an increase in the transverse section of the muscle. In such a tract the current enters the natural ends of all the added fibres of the muscle, and the density with which it enters is much less towards the equator of the muscle than it is towards the end. In this last position the density of the current would perhaps be sufficient to produce positive anodic polarisation, whereas in the former position it only shows negative polarisation. The anodic tract will therefore show, after breaking the stimulating current, polarisation in two opposite directions. As the semimembranosus has fresh accessions of fibres far up, the circumstances above mentioned demand consideration.

There is always a similar condition when a current enters a muscle composed entirely of parallel fibres, not at its natural end but at the side, even if the current meet with no fresh fibres on its way. The current enters those fibres which are in the immediate neighbourhood of the stimulating anode with greater density than those which are more remote. It is further to be noted that only a portion of the current which enters a particular fibre flows on into it, the rest passing on to fibres more remote from the stimulating anode. It is therefore first necessary to know exactly the laws of transverse polarisation, in order to be able to say to what extent in this case kathodic polarisation can take place along with anodic. In any case, there is a preponderance of anodic polarisation (as would be supposed theoretically, and as can be practically demonstrated), and I have therefore considered it alone in the above pages. Sufficient has been said to show how difficult or impossible it is to unravel the intricacies of the different individual polarisations which must have existed in du Bois-Reymond's experiments.

One other result on which du Bois-Reymond seems to lay great weight remains to be considered. In a special series of experiments he brought one galvanometer electrode to the equator of the pair of muscles, whilst the other was placed either immediately above the lower or below the upper stimulating electrode. The stimulating electrodes, if I understand rightly, were placed near the ends of the muscle. Thus the polarisation-current was led off either entirely from the upper or entirely from the lower half of the muscle. It now resulted that the upper half showed stronger positive polarisation when the current was ascending than when it was descending, whereas the lower half gave stronger positive polarisation when the stimulating current flowed from above downwards.

Let us for the moment imagine that the upper and lower halves of the pair of muscles were strictly symmetrical, both tendinous intersections passing exactly through the equator, that the stimulating electrodes were arranged symmetrically, and, finally, that one electrode lay on the equator, the other alternately on symmetrical spots of the upper or of the lower half of the muscle. In this case any one who knows that polarisation phenomena depend not on internal polarisation but on changes occurring at the points where the current enters and leaves the muscle, would readily see that the upper half must necessarily be in the same relation to the ascending current in every respect as the lower half is to the

descending, and *vice versa*; for the direction of the current in the first case would have exactly the same significance as regards the first half, as the opposite direction of the current in the second case would have as regards the second half, because being symmetrical the one half would be the exact reflection of the other. In like manner it would be expected that each individual half would behave in general differently towards the two directions of current, because in each half there would be no symmetry of structure in the up and down direction.

Du Bois-Reymond's muscle-preparation deviates widely from the strictly symmetrical muscle scheme above described, yet there is an essential analogy, in so far as there are tendinous intersections passing through the middle of both muscles, and as the pair of muscles taper away above and below. The result of du Bois-Reymond's experiments does not therefore surprise us at all, whilst to him it appeared striking and of great import.

The same thing may be said as to the further observation of du Bois-Reymond, that the strength of the secondary electromotive actions in both halves of the pair of muscles (or even in the gracilis alone) was not equal. The simple reason of this is, that the two halves of the muscle are not exactly symmetrical in relation to the equator; the tendinous intersections do not lie in the equator itself, nor is the configuration of the upper half of the pair of muscles (or of one of them) the exact reflection of the lower. Moreover there could scarcely be a muscle adapted to this kind of research, of which both the external and internal structure would be strictly symmetrical. We should only have been surprised if du Bois-Reymond had found the strength of the secondary electromotive phenomena to be always equal in the two halves of the muscle, whereas the opposite result is what might have been anticipated.

In answer to the final point emphasised by du Bois-Reymond, that when the galvanometer electrodes are placed symmetrically on the muscle, so that one is below the upper stimulating electrode, the other above the lower one, the polarisation-currents are not equal in both directions, it must also be said that it would be strange if they ever were equal. So long as we start with the assumption of an internal polarisation of the whole tract through which the stimulating current flows, all inequalities of polarisation dependent on the direction of the stimulating current, must continue to afford new and enigmatical problems.

Among these difficulties may be mentioned the difference in strength of the polarisation-currents according to the direction of the stimulating current in the pair of muscles, and the fact that the relations of the polarisation-currents led off from the upper half of the muscle are in some respects the reverse of those led off from the lower half. Another question is, why the positive polarisations in each half are stronger when the stimulating current flows from the equator towards the extremity, than when it flows in the opposite direction, and why the reverse is not the case? and why, further, all secondary actions are stronger in the lower half of the muscle than in the upper? why very strong descending currents (30 to 40 Groves) with closing times of 20 secs. 1 min., 5 mins. again give positive variation, ascending currents negative variation, and so on? For each of these questions I could find an answer based on the experience I have gained in working with the sartorius. That such answers would be correct as regards the pair of muscles in question, could only be proved by the aid of numerous and varied researches on them. I cannot however regard it as my task to institute a tedious series of researches under such complicated conditions as those offered by du Bois-Reymond's preparation. Such researches could at best only lead by a long and circuitous path to such a knowledge of the same laws as is afforded directly by the study of a regularly constructed muscle.

With the observation just mentioned, that with certain current strengths and closing times the positive polarisation was stronger in each half of the muscle when the current flowed in that half from the equator to the end, du Bois-Reymond connects the supposition that this phenomenon stands in relation to the circumstance, that in natural stimulation of a muscle through the nerve, the excitation spreads from the neighbourhood of the equator where the nerve-filaments enter the muscle-fibres, towards both ends. Hence he infers that the direction in which normally the proper physiological changes are propagated in muscle-fibres is the most favourable likewise for positive polarisation.

It is not however clear how the observations of du Bois-Reymond on his muscle-preparation could lead to such a supposition. For each muscle of the pair, on account of the tendinous intersections, consists functionally of two separate muscles. With regard to the rectus internus major or gracilis this is strictly true; with regard to the semimembranosus, it is at least partly so, for only some of its fibres run the whole length of the muscle, all the others

either end or commence in the tendinous intersection. Hence the stimulus imparted by the nerve would not start from the neighbourhood of the equator of the pair of muscles, i.e. from the region of the intersection, but each half being functionally a muscle of itself would have its own equator.

It would be contrary to all analogy if the motor end plates were especially crowded together in the vicinity of the intersections; this would be much more likely to be the case in the neighbourhood of the equator of each individual half of the muscle, with the exception of the long fibres of the semimembranosus. Instead of comparing the positive polarisation in both halves of the muscle, du Bois-Reymond ought to have investigated each quarter of the muscle for comparison. In the first and third quarters, counting from above, the ascending positive polarisation ought to have proved strongest, in the second and fourth the descending, if the experimental evidence was intended to support the suggestion of a connection between functional direction and positive polarisation.

For the rest in Sect. 21 of his paper (No. VI), du Bois-Reymond makes no further statement about the muscles with which the researches were actually conducted, when he says, 'In regular monomerous muscles (i.e. those consisting of longitudinal fibres only) positive polarisation is stronger in the direction from the equator towards the ends, than in the opposite direction.' No experiments however on monomerous muscles are contained in the whole treatise, but only those already mentioned with the rectus internus and semimembranosus, which are pre-eminently 'pleiomerous' muscles, i.e. such as have fibres commencing and terminating within their limits. Moreover, had du Bois-Reymond repeated his experiments with monomerous muscles, he would have found the true condition to be the reverse of his statement with regard to them, viz. that with stimulating currents of relatively equal strength (and corresponding density) and of the same short closing time (0·32″) he would have found positive polarisation in the half of the muscle next the stimulating anode, none or weak negative polarisation in the half next the stimulating kathode, and through which therefore the current flowed in the direction from the equator towards the end. Had du Bois-Reymond instituted such experiments as these, he would at once have recognised that the muscle is not polarised in the same direction in the whole intrapolar tract (see below).

In du Bois-Reymond's speculations as to the connection between positive polarisation of muscle and the direction in which the

wave of contraction liberated from the nerve flows, there appears to me to be a contradiction which is the more inexplicable from the fact that he described the structure of both muscles used by him, and especially mentioned the circumstance that each half of the muscle received its own special nerve supply.

II.

Du Bois-Reymond informs us at the end of his treatise that he was acquainted with positive polarisation of muscle long before the issue of the first volume of his 'Researches' (1848), and that from it he was led to the conception of the electromotive phenomena of nerve and muscle. From positive polarisation of muscle he was led to a similar conclusion with regard to the intrapolar tract of nerve, and a few years later he actually discovered the intrinsic polarisation of nerve which before he had only assumed theoretically.

'In so far as no other reasonable explanation of positive polarisation could be given,' continues du Bois-Reymond, 'excepting that which regards it as due to the directing of already existing forces, the evidence obtained of this polarisation is at the same time serviceable in another way. In my eyes it afforded and will continue to afford proof of the presence of electromotive forces in uninjured nerves—proof which in the absence of a natural transverse section of a nerve was otherwise lacking. The evidence of the existence of such forces in muscle, obtained by carefully testing the natural transverse section of muscle, is also strengthened by it.' Hence, in internal positive polarisation, according to du Bois-Reymond's own assertion, we are expected to see the origin and mainstay of his whole theory of nerve- and muscle-currents. Here again I find myself compelled, by means of a series of experimental examples, to show that intrapolar positive polarisation in du Bois-Reymond's sense cannot be demonstrated.

I begin with an experiment in which the stimulating electrodes were placed on the muscle in the same manner as they were in du Bois-Reymond's experiments, although this method of leading in the current is not generally to be recommended for reasons given above. Instead, however, of a muscle divided by a tendinous intersection, I used a curarised sartorius, which, according to Aeby's researches, is in most cases though not invariably really monomerous, which matter I discussed in my twelfth communication[1] (see p. 229).

[1] [Not included in the present series of translations. See Preface. ED.]

This muscle, stretched by the clamping of the pelvis and tibia, lies horizontally with its borders directed upwards and downwards. As the muscle tapers away by termination of fibres towards its lower attachment, I place the lower electrode at the junction of its middle and lower thirds, the upper one ½ cm. below the upper end on the wide surface of the muscle. Exactly opposite both these electrodes, on the other wide surface of the muscle, I place the galvanometer electrodes—one opposite each. Midway between these two, on the same surface, a third galvanometer electrode is applied. In rapid succession, the lower and upper electrodes, or the lower and middle, or the middle and upper can be thrown into the galvanometer circuit, so that alternately the whole of the intrapolar tracts, or only the lower or only the upper half of the muscle is in circuit. All the electrodes are tube electrodes. I use the whole current of 7 or 8 Daniells for stimulation. The period of stimulation is 5 secs., the 'transmission time' ·026 to ·034 sec. A current of this strength, with this period of stimulation with a fresh, well-excitable muscle and electrodes arranged as above, gives strong positive anodic and weak negative kathodic polarisation.

If immediately after opening the stimulating current I throw in the lower half of the intrapolar tract next the stimulating anode, I get a strong positive polarisation current; if I throw in the upper half next the stimulating kathode, I get a weak negative polarisation current. If, finally, after opening the stimulating current I throw the whole of the intrapolar region into the galvanometer circuit, this gives a polarisation current corresponding to the *difference between the positive anodic and the negative kathodic polarisation*, making allowance for the change of resistance caused by the introduction of a longer tract of muscle. Naturally it would be best if after one and the same stimulation the polarisation of all three tracts could be measured separately, but simultaneously. As this is impossible, it is necessary to make several experiments on the same muscle. Each preceding experiment influences that which follows it. This circumstance only changes to some extent the strength, not the direction of the individual polarisation currents. In these experiments we have to deal not with subtle but with relatively substantial phenomena. To eliminate the influence of the order in which the three tracts are investigated, either researches are made with several muscles in different order, or a series of experiments is repeated in reversed order on the same muscle, as was partly the case in

the researches tabulated below; but the direction of the current must not be changed in the course of an experiment. For, so strong a current at its point of exit, impairs considerably the susceptibility of the muscle substance for positive anodic polarisation. Thus, when in an experiment the spot of muscle which had acted as the point of entry for the descending current, served as the point of exit for the stimulating ascending current, it showed much weaker positive polarisation, and might even show negative polarisation, a circumstance of which I made mention in the preceding communication. An exactly analogous experiment can be made on another muscle with a descending current; it is best to use the other sartorius of the same frog.

The following table gives examples of such a series of experiments. The Roman numerals correspond to the order of the individual experiments on the same muscle :—

1.

Ascending current. 7 Daniells. Closing time 5 secs. Transmission time ·026 sec. to ·034 sec.

	Entire intrapolar tract.	*Lower half of intrapolar tract.*	*Upper half of intrapolar tract.*
I.	+220		
II.		+342	
III.			−45
IV.		+287	
V.	+177		
VI.			−43
VII.	+123		

2.

Descending current. 8 Daniells. Closing time 5 secs. Transmission time ·026 sec. to ·034 sec.

	Entire intrapolar tract.	*Lower half of intrapolar tract.*	*Upper half of intrapolar tract.*
I.	+200		
II.			+300
III.		−35	
IV.			+239
V.	+136		
VI.		−26	

With weaker currents and the same arrangement, negative kathodic polarisation outweighs positive anodic, so that the current led off from the whole intrapolar tract is negative, of which an example may be given :—

3.

Descending current. 4 Daniells. Closing time 5 secs. Transmission time ·026 sec. to ·034 sec.

	Entire intrapolar tract.	*Lower half of intrapolar tract.*	*Upper half of intrapolar tract.*
I.		−92	
II.			+60
III.	−30		

After such experimental results no one will be disposed to maintain that the entire intrapolar tract is internally polarised in the same direction. The utmost that could be supposed with regard to that matter, is that one half undergoes internal positive the other internal negative polarisation, or that both are positively and negatively polarised at the same time, but in such a manner that the positive is in excess at the anodic half, the negative at the kathodic half of the intrapolar tract. This would be a totally different kind of polarisation of the intrapolar tract from that assumed by du Bois-Reymond.

Admitting, however, the existence of an internal polarisation in opposite directions of the two halves of the intrapolar tract, it can be conclusively shown that such a polarisation could not be generated by the current within the intrapolar tract, but must be caused by a change of the muscle substance propagated from the anodic or kathodic spots to the intrapolar tract. For if the anodic spots of the muscle which showed strong positive anodic polarisation be destroyed, without making any other alterations in the arrangement of the apparatus, and if then the same stimulating current be again sent through in the same direction, there is no positive but at the utmost weak negative anodic polarisation on breaking the current.

I have performed this experiment in various ways, and always with the above result. For instance, the stimulating current was led through the bones to the horizontally extended sartorius, and one

electrode was placed on the middle of the muscle, the other on its attachment to the pelvis. After breaking the descending current the positive polarisation current was measured. The upper end of the muscle was destroyed by means of a heated glass rod, with which it was touched in the region of its natural section. After the muscle was thus destroyed I replaced the upper electrode on the same spot. On heating the muscle it thickened, and now the current no longer flowed into the living muscular substance through the short tendon, but through the dead portion. Thus the density of the current was now less at its point of entry into the living portion of muscle than it had been previously. On this account, in the experiment with the uninjured muscle, I placed on both sides of the tendon, in the groove between the muscle substance and the bone, a piece of blotting-paper folded four times and steeped in normal salt solution. By this means the density of the current was decreased at its point of entry into the muscle substance. A current from 4 Daniells was now sent through the muscle for 5 secs. in a descending direction, with the result, to quote a particular instance, of positive polarisation to the extent of 129 degrees of the scale [1]. After this the upper electrode was removed, the end of the muscle was destroyed, and the electrode again replaced. The strong descending demarcation-current of the muscle now flowed into the galvanometer-circuit. As soon as the muscle had cooled and its current had become constant, this was compensated, and the same current as before was again sent through for 5 secs. in a descending direction: there was now negative polarisation to the amount of 13 scale.

I also made similar experiments with the current led in from the side. Let it be imagined that the two electrodes are placed on one of the wide surfaces of the muscle at moderate distances from the ends, that one galvanometer electrode is directly opposite the upper stimulating electrode, the second in the middle of the muscle. With this arrangement I obtained, for example, with a descending current of 8 Daniells closed for 5 secs. after the first stimulation, a positive polarisation current amounting to 300 scale; after the third, a similar one still amounting to 239 sc.

Hereupon the upper stimulating electrode and the upper galvanometer electrode were removed, the spots of muscle on which they had rested were destroyed on either side with a heated glass rod, then

[1] Two excitations with the ascending current had preceded this, hence positive polarisation was already diminished.

moistened with ·6 per cent. salt solution, and the two electrodes replaced in their respective positions. After the strong descending 'demarcation' current had become constant, it was compensated, and the muscle was again stimulated for the same period with the same descending current; on breaking, negative polarisation resulted to the amount of 36 divisions of scale.

In destroying the muscle by heat it is necessary to defer exciting anew until the heated portion cools down. The result is the same if the muscle is locally destroyed by crushing with a pair of pincers. After crushing the lower end of the sartorius, I obtained only slight negative anodic polarisation, with ascending currents of the same strength and duration as those with which I had obtained positive anodic polarisation, amounting to far more than 100 divisions of the scale, from the uninjured lower end of the muscle. And even with the whole current from 2 Daniells and with 10 secs. closing time, I obtained only weak negative polarisation to the amount of 20^{sc}, whereas when the lower end of the muscle is in a normal condition, the whole current is wont to give such a strong positive anodic polarisation current, even with short closing time, that the image of the scale shoots out of sight. The difference of action before and after destruction is in this case more prominent, because the current enters the normal lower end of the muscle with greater density than it does the living muscle substance above the crushed end. That the muscle substance lying above the lower destroyed portion, and that lying below the upper destroyed portion as well as the whole remainder of the uninjured muscle, has not lost its susceptibility for positive anodic polarisation, can be easily shown by control experiments.

The fact thus established, that the stimulating current which passes through dead and dying muscle substance to enter muscle which is still excitable and living, is not in a condition to produce positive anodic polarisation in the anodic spots of the latter, as well as the fact shown in Biedermann's researches that it is incapable of producing the break-contraction, proves that the cause of so-called positive polarisation must be sought for, for the most part if not exclusively, not in changes which the current directly produces in the whole or in some part of the intrapolar tract, but in changes taking place at the anodic spots of the muscle substance, which spread more or less from the latter into the former. *The positive polarisation-current is thus dependent upon the integrity of the anodic spots of the excitable substance.*

That weak positive anodic polarisation can be obtained by passing excessively strong currents through a destroyed spot into the muscle, is on obvious grounds not to be doubted; but weak break-contractions are also obtained under those circumstances.

Negative kathodic polarisation becomes almost impossible when the point of exit of the current is killed, provided that its strength and duration are not too great.

Experiments in which the electrodes are applied to the surface of the muscle have the disadvantage, that the strength of the polarisation phenomena, with equal strength of stimulating current, must depend on the extent of surface of contact of the electrodes. For it is this which determines the density with which the current enters or leaves the muscle, and on this density the strength of anodic and kathodic polarisation depends. Even if the density of the current is equal throughout the intrapolar tract, i.e. the tract in which the fibres are parallel, yet it may be different at the spot of entry or exit, and at the same time the strength of the polarisation-current may be very different, whereby the measurement of the intensity of the stimulating current loses much in value. It is also of no little importance, as has already been explained above, that the current enters the fibres cross-wise or obliquely, and that nearly all the fibres are traversed by portions of current, and therefore have both anodic and kathodic spots.

Tschiriew[1] has of late given an account of experiments made with the sartorius, in the results of which he sees confirmation of du Bois-Reymond's theory. He laid both stimulating electrodes on one surface of the muscle, both galvanometer electrodes (Fleischl's brush electrodes) exactly opposite them on the other surface, so that the intrapolar tract amounted to about 15 mm. He obtained, 'with short periods of closure of the polarising current—up to 4 secs. and sometimes more—and with the freshest possible preparations, purely positive excursions of the needle. With a longer closing time, and when from the duration of the experiment the excitability of the preparation had decreased, the excursions became diphasic, a negative deflection preceded the positive, and finally a purely negative polarisation remained.' As appears from a table of experiments, Tschiriew changed the direction of the current from one experiment to another in the same series[2]. The change in the direction of the current made the spot of the muscle

[1] Archiv f. Anat. u. Physiol. 1883. Festschrift, Suppl. Vol. p. 284.

[2] The explanation of his results follows naturally from what I have already said.

which was in contact with one stimulating electrode, first the point of entry, then the point of exit of the stimulating current. Through the kathodic action of the current the susceptibility of the muscle for positive anodic polarisation was soon diminished in the neighbourhood of both the stimulating electrodes, so that the preponderance of negative kathodic polarisation kept increasing, and at the same time there was negative polarisation even at the anode.

As the whole intrapolar tract was included in the galvanometer circuit, only the algebraic sum of the anodic and kathodic polarisation-current would find expression in the deflection of the magnet. I adopted substantially Tschiriew's method in my earliest experiments on polarisation of muscle. I applied to the under surface of the horizontally extended muscle, across its long axis, two small cylinders of the clay used for electrodes, these cylinders being in contact on one side with the stimulating electrodes, on the other with the galvanometer electrodes. This arrangement has the advantage over that of Tschiriew, that the polarising currents enter and leave the muscle at the same points as the galvanometer-currents. In comparison with du Bois-Reymond's arrangement, Tschiriew's has the advantage that the polarisation currents recorded were always the result of two polarisations, one anodic, the other kathodic, whilst in du Bois-Reymond's experiments, besides the two polarisations in the neighbourhood of the stimulating electrodes, the considerable polarisations at the tendinous intersections come into account.

I also made some experiments with du Bois-Reymond's muscle preparation, as well as with the muscle which he calls gracilis, by itself, introducing the current through the bones. With this arrangement from one and the same muscle, with the same intensity and strength of current, I obtained polarisation currents which were of different strengths and differently directed, according as I applied the electrodes to one or another spot of the muscle, keeping the electrodes in all cases about 1 cm. apart. This was the case whether I used the same pair of electrodes, and shifted them before each new stimulation, or whether I used several pairs of electrodes, and connected them alternately with the galvanometer, as described above for analogous experiments. The confusion of differently directed or diphasic polarisations was so great that I did not feel tempted to pursue the matter further. If the electrodes are always applied in the same position to the muscle, the polarisation currents must necessarily follow a certain law.

Du Bois-Reymond called the closing time which was necessary with a definite strength of stimulating current and a fresh preparation, in order to obtain polarisation in alternately opposite directions, the 'critical time.' (See No. VI. Sect. 9.) Shorter closing times gave with the same stimulating current positive polarisation, and longer, generally negative. Under special conditions, as when descending currents of 30 to 40 Groves were used, positive polarisation reappeared. After all that has been said, the determination of this 'critical time' has no great value. In anodic polarisation, however, a critical closing time might be spoken of, inasmuch as with fresh muscle and weak stimulating currents the polarisation is negative with short, positive with longer closing times. Even if it were possible always to produce equal density of current at the anodic spots in a series of experiments on fresh muscles, this 'critical time' would depend essentially on excitability of the muscle, which varies greatly even in frogs which have been kept under the same conditions.

I cannot yet speak of a 'critical time' for kathodic polarisation as I have not yet succeeded in demonstrating positive kathodic polarisation. By applying the electrodes to the sides of the preparation, in which case the stimulating current traverses the fibres transversely or obliquely, I have repeatedly observed diphasic polarisation, and once indeed positive kathodic polarisation. As, however, with this method of leading in the stimulating current, the greater number of the fibres of the muscle must contain both anodic and kathodic spots in the neighbourhood of the kathode, and as the density of current is not the same in the former as in the latter, it is not surprising that we get in this case diphasic polarisation. But, on this point, I can at present express no definite opinion, because, as I said, I have seldom employed the lateral method of leading in, which is in general unadapted to the purpose, and therefore I possess no series of experiments as to the polarisation which occurs when this method is employed. The discussion of this question must be the object of special researches on polarisation with transverse and oblique currents.

Du Bois-Reymond avoided leading in through the natural ends of the muscle, because he feared the secondary resistance pointed out by himself in the thin tendons, considering that as 50 Groves were used, and the closing times amounted to 5 min., this must have been considerable.

In our experiments, which were made with at the most

8 Daniells, the question of secondary resistance was of the less importance, as from the first it proved to be unnecessary to exercise any strict supervision of the strength of the stimulating current. Accordingly we did not spend much time in measuring it. In more minute experiments, however, this would occasionally be necessary.

It must not be thought that our researches are not comparable with those of du Bois-Reymond because we used relatively much weaker currents. The question here is not of the intensity, but of the density of the current in the muscle, and this is incomparably greater at the natural ends, especially at the lower end of the sartorius, with the same strength of current, than at the thick portion of the pair of muscles used by du Bois-Reymond; and this holds good notwithstanding that the sartorius, when the current is led in through the bones, offers a much greater resistance than the pair of muscles does when the current is led in laterally. Hence it is only those experiments conducted by du Bois-Reymond with extraordinarily strong currents which cannot be at once brought into comparison with ours.

If the care and accuracy with which du Bois-Reymond is wont to conduct his experiments, as well as the acuteness with which he designs and interprets them, be taken into consideration, it will appear surprising that so distinguished an observer should have fallen into so fundamental an error, an error which derives its importance from the circumstance that he founds on it his whole theory of nerve and muscle currents. I find the cause of the error mainly in the fact that du Bois-Reymond has not devoted the same thorough study to the mechanical effects of excitation of muscle as he did to the electrical effects. Among other indications this appears from the fact that in 1881 in his work on the researches conducted by Dr. Sachs on the Gymnotus, he remarks[1] cursorily that 'in direct stimulation' (with the electric current) 'contraction commences at all points of the muscle at the same moment.' Quite apart from the researches referring to this matter of Bezold and Engelmann, Biedermann in 1879 brought conclusive evidence of the fact that it is not so, but that the make-contraction commences at the kathodic, the break-contraction at

[1] Dr. Carl Sachs, Untersuchungen am Zitteraal. Leipzig, 1881, p. 226.

the anodic spot of the muscle. Accordingly contraction can only be supposed to commence simultaneously throughout the whole intrapolar tract when the currents are of greater density in the muscle than the strongest currents used by Biedermann.

Had not du Bois-Reymond adhered to the old view of simultaneous stimulation in the whole intrapolar tract, had he even regarded as an open question that of the starting-point of excitation in direct electrical stimulation, he would scarcely have employed in his experiments on polarisation muscles divided by tendinous intersections. At the same time it was an unfortunate circumstance that the very muscles which he chose on account of certain advantages presented by them should have been traversed by tendinous intersections, for had those intersections not been present, du Bois-Reymond would certainly have recognised the error of his assumption, at all events in those experiments in which he led off the polarisation-current from one or the other half of the intrapolar tract.

In a future communication I shall have to speak of du Bois-Reymond's researches on secondary electromotive phenomena in nerve.

VIII.

ON

THE POSITIVE VARIATION

OF THE

NERVE CURRENT AFTER ELECTRICAL STIMULATION.

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VIII.

THE investigation of negative variation of the nerve current, with the improved methods for which we are indebted to du Bois-Reymond, leads to results which modify in many respects the doctrines taught by its discoverer respecting it.

I may premise that in future communications I shall frequently have the opportunity of recurring to the negative variation, and shall confine myself here to a short discussion of the fact that the negative variation of the nerve current caused by electrical tetanisation is generally followed by a positive variation, which commences at the close of the stimulation and thus immediately follows the negative variation.

Du Bois-Reymond's statement, 'that after tetanic stimulation the needle of the multiplier only returns more or less incompletely to its state of rest,' a phenomenon which he attributes to loss of electromotive power of the nerve in consequence of the preceding stimulation, accordingly appears to be insufficient. My observations were made in December and January, partly with cold, partly with warm frogs (R. esculenta); the former term I apply to frogs brought straight from the cellar, the latter to those kept for some days in a room the temperature of which never fell below 15°C.

The tract of nerve lying between the stimulating electrodes I call the stimulated region. It always consists of a portion of the sciatic plexus a little below the ligatured upper end, and was 5 mm. in length. The portion lying between the leading off electrodes will be designated the galvanometer tract. It is always at the peripheral end of the nerve. The portion between the lower stimulating electrode and the upper galvanometer electrode will be called the intermediate tract.

Unpolarisable electrodes were almost exclusively employed. The lower ends of these were filled with saline clay, into which was introduced a brush steeped in ·6 per cent. salt solution. An ordinary camel-hair pencil was used, and this was cut off about 1 cm. above the lower end of the quill. If there are several such brushes at hand, it is easy to find one to suit any electrode tube, fitting firmly into it. These electrodes are made like the pencil electrodes of Fleischl, with this difference, that modelling clay serves instead of gypsum to close the lower extremity. This material is easily renewed after each experiment. These electrodes are only occasionally completely free from current. I therefore measured this current, before each experiment, by bringing the two points into direct contact. Its strength is given in each case in the experiments hereafter quoted. As we are dealing with nerve currents, the galvanometer used was very sensitive. Consequently the electrode deflection was sometimes considerable; but it must not be forgotten, however, that after introduction of the nerve with its great resistance into the circuit, the current of the electrodes has not nearly so marked an effect on the deflection of the needle caused by the nerve current, as it would have had without that increase of resistance. On the amount of negative or positive variation observed after compensation of the nerve current, the current of the electrodes has no influence; I therefore took no further pains to secure perfectly unpolarised electrodes, although these are indispensable in other cases. If a larger number of electrodes be prepared on the type above described, two may generally be found which are quite, or nearly devoid of current at least for a time. The stimulating currents were also introduced by these electrodes. A moist chamber protected the nerve from drying, but unavoidably favoured unipolar action. Very weak stimulating currents were therefore used and numerous control experiments were made, especially those in which the nerve was crushed in the intermediate tract. The secondary coil (5000 turns) of the induction apparatus (worked by 1 Daniell) was scarcely ever brought nearer than 20 cm. to the primary, under which condition unipolar action was not noticeable. In spite of the resistance of the electrodes, the induction current thus obtained proved quite sufficient. On account of the many drawbacks to the ordinary induction apparatus in use in physiological laboratories, the following method was employed to produce induction currents.

In order to obtain reversed but physiologically equal currents, a few years ago I improvised the following apparatus. A secondary

coil of 7110 turns was mounted so as to revolve on a vertical axis. The ends of the spiral terminate in slender plates running in circular troughs filled with mercury, of which one is placed above, the other below the revolving coil. These channels communicate with the stimulating electrodes. The coil is made to revolve by means of a pulley. If a strong magnet or the primary coil of an induction apparatus through which a current is passing, be brought into the neighbourhood of the revolving coil, and if the rate of revolution is high enough, currents in alternately opposite directions are obtained, which are sufficiently strong and physiologically equal. The strength of the currents may be varied on the one hand by changing the number of elements which supply the primary current, on the other they may be adjusted with the utmost delicacy by altering the position of the primary coil or magnet. With only 1 Daniell and 20 revolutions per second, I got tetanus with sensitive preparations when the axes of the two coils (when parallel) were 9 cm. distant from each other, the most superficial layers of the two coils being 25 mm. apart. In the experiments I am about to describe, 3 Daniells gave the primary current, the coils were as near together as possible, and the number of revolutions amounted to about 20 per second, corresponding to twice as many induction currents.

An induction apparatus was also used in which the primary coil was replaced by a single conducting ring. A flat wooden ring (vulcanite would have been a better material) was made 87 mm. in diameter and 30 mm. in width. Around this 1120 turns of thin copper wire were wound. Then a second ring was made of the same width but somewhat larger. This encircled the first ring, and a space was left between the two for a thin copper ring 104 mm. in diameter. The copper ring was nearly the same width as the wooden rings (25 mm.). A slit was made in it so that it did not form a closed circuit. It consisted of a circularly bent strip of copper, the ends of which were brought into electrical continuity by means of terminals which communicated with wires from the battery. The primary circuit thus constituted required a special interrupter. For this purpose, I used either a wheel provided with twelve copper points which passed in quick succession through a vessel of mercury, or one of Wagner's hammers adapted for the purpose. This was set in action by a special cell, and besides interrupting its own current, effected the regular interruption of the above-mentioned primary circuit. The introduction of the hammer into the primary circuit as in the ordinary induction apparatus is inadmissible here, for if the coil of

the electromagnet were in the primary current, extra currents would be produced which it is desirable to avoid. The turns on the outer ring together with those on the inner ring form the secondary coil. In consequence of the close proximity of all the turns of this double coil to the inducing ring of copper, even 1 Daniell is quite sufficient to obtain tetanus from a sensitive nerve-muscle preparation. In the experiments which we are going to consider, 3 Daniells were used. In order to ensure the possibility of varying the strength of the induction currents, the copper ring is made moveable, and can be partly or entirely removed from the rings of the secondary coil.

Although this induction apparatus is preferable to the ordinary one in all experiments where it is desirable to obtain an equal duration of the make- and break-currents, yet it shares with it some of the disadvantages connected with the mode of interruption, particularly that the interval between the make and the following break is not quite equal to that between the break and the following make, unless a special contrivance is used for the purpose. Moreover, exact equality between make- and break-currents was not obtained.

The apparatus I use is only intended for the stimulation of nerve. The strength of the currents can however be increased, with the same number of turns, by increasing the diameter of the rings. I also stimulated with ascending and descending break-currents of an ordinary induction apparatus, the make currents being cut off. Finally, interrupted battery-currents ascending, descending, and alternately in opposite directions were employed to stimulate the nerve. In all cases the positive variation of the nerve current was clearly demonstrated. All experiments were made with a Wiedemann's galvanometer with the magnet aperiodic. This instrument is not especially well adapted to these experiments, because the time which the magnet takes in coming to rest is too great in proportion to the duration of the positive variation. I shall take some opportunity of repeating the experiments with a galvanometer more suited to the purpose. So much of the phenomenon as I am now concerned with can be satisfactorily examined with the above-named galvanometer.

The positive after-variation may be investigated by three distinct methods.

1. Without a compensator, the nerve current is led off from the lower end of the nerve, and a short period is allowed after the magnet has taken up its new position in order to be assured of the constancy of this current. When this is satisfactory, the nerve is tetanised near the other end. As a result of stimulation the magnet swings back for a certain distance. At the end of excitation, the magnet returns to and even passes beyond the position which it had before stimulation, but as a rule comes back immediately, and slowly regains its original position. The positive after-variation is now over.

It is here of course understood that the magnet swings aperiodically, otherwise its excursion beyond the original deflection would afford no proof of a transitory increase of the nerve current. I give an example of experiments conducted in this manner:—

Warm Frog. Du Bois-Reymond coil. Galvanometer tract 5 mm. Intermediate tract 30 mm.

Deflection caused by current of electrodes . .	500 to 510.
,, nerve current	500 ,, 621 = +121.
Duration of stimulation 10 secs. Return of magnet .	,, 609 = −12.
Deflection at close of stimulation . . .	,, 625.
Immediate return of magnet	,, 621.
Positive after-variation therefore amounts to . .	+4.

2. Experiments conducted with the nerve current compensated are much preferable to the above. The negative variation of the nerve current is now shown by deflection of the magnet in the opposite direction under the influence of the compensation current. At the close of stimulation, the magnet not only returns to its position of equilibrium, but passes beyond it, and then immediately, or after a very short interval comes back and slowly regains its original position. This concludes the positive after-effect. When the object is not to observe the whole course of the positive after-variation, it is desirable to break the circuit of the galvanometer as soon as the positive effect has arrived at its maximum, and the magnet is on the point of returning; for in this way it is more easy to make sure that the magnet has not spontaneously changed position during the period of the two deflections.

The following is an example:—

Cold frog. Du Bois-Reymond coil. Galvanometer tract 10 mm. Intermediate tract about 30 mm.

The Roman numerals in this and in the following table refer to the order of the individual stimulations. The number with a minus sign gives the diminution of the nerve current during stimulation, that with a plus sign gives the amount of transitory increase of the nerve current at the close of stimulation. The duration of stimulation is given in seconds in each case.

Current of electrodes +40°. Nerve current +154°.

I. 5 secs.	$\begin{cases} -15 \\ +2 \end{cases}$	III. 10 secs.	$\begin{cases} -1 \\ +5 \end{cases}$
II. 5 secs.	$\begin{cases} -14 \\ +3 \end{cases}$	IV. 20 secs.	$\begin{cases} -16 \\ +8{\cdot}5 \end{cases}$
		V. 20 secs.	$\begin{cases} -16 \\ +6{\cdot}5 \end{cases}$

Cold frog. Stimulation with rotation apparatus. Galvanometer tract 8 mm. Intermediate tract 38 mm.

Current of electrodes +7. Nerve current +195.

I. Duration of stimulus 15 secs.	$\begin{cases} -41 \\ +12 \end{cases}$	
II. „ „ „	20 secs.	$\begin{cases} -38 \\ +9{\cdot}5 \end{cases}$

The increase of nerve current after close of stimulation is a transitory one. I often noticed that the magnet, when negatively deflected during the stimulation of the nerve, suddenly moved in an opposite direction at the moment the stimulation ceased, this movement being out of relation with the final amount of the deflection: thus it seemed probable that the positive increase of the nerve current is greater immediately after stimulation than it appears to be from the weak positive deflection which the magnet eventually shows, that is, that before the dilatory magnet as it slowly returns to zero has reached that point, an appreciable amount of the positive increase of nerve current may already have been spent, so that only the remainder conducts the magnet through its position of equilibrium to a position of positive deflection. From this may be explained the fact that occasionally, and especially with feebly excitable or fatigued nerves, the positive deflection is quite lost when this method of observation is adopted.

3. Hence it is desirable, after accurate compensation of the nerve current, to open the galvanometer-circuit during stimulation and only to close it again immediately after ceasing to stimulate. This plan has another advantage, viz. that a portion of the compensation current corresponding in amount to the negative variation is prevented from passing through the nerve during the period of

stimulation. This is the third and by far the best method of investigating the positive after-variation. In this case an aperiodic magnet is unnecessary.

With investigations carried out in this manner, the correctness of the above supposition was shown, in so far that I got appreciably stronger positive deflections than when the galvanometer-circuit was closed during stimulation. In this investigation I used the same double switch which I used for the researches on polarisation described in my twelfth contribution.

In one position of the switch the stimulating circuit (in this case generally the circuit of the secondary coil) is broken in two places, while the galvanometer-circuit is closed; in the other position the galvanometer-circuit is broken in two places, while the stimulating circuit is closed. From this last position the switch is reversed in such a way that the time of its passage, i.e. the interval between the opening of the stimulating circuit (end of stimulation) and the closing of the galvanometer-circuit was always the same. In our experiments it amounted to between 0·026 and 0·034 of a second [1].

With this method of investigation a determination of the amount of negative variation is not obtained. For this purpose two observers and two galvanometers, each with a special compensator, would be necessary. The electrodes conducting the nerve current would have to be arranged by means of a switch so as to permit of their being connected now with the one, now with the other galvanometer. In both galvanometers the nerve current would have to be compensated. On one the negative variation would have to be observed, and at the end of stimulation the electrodes would have to be quickly connected with the other galvanometer, on which the positive variation would have to be read. At the same time the above-mentioned drawback is to some extent remedied, if observations are made with the same nerve and with equal strength and duration of stimulation alternately according to the third and second methods. If it is desired to make an observation according to the second method after one has been made according to the third, it is only necessary,

[1] It is not to be understood that the transmission time varied between these limits; I can even venture to say that it was always tolerably nearly the same. The method which I adopted to determine the time in question does not permit of direct measurement of that time, but gives on the one hand a duration which the transmission time cannot possibly exceed, on the other hand a duration of which it cannot possibly fall short. Whether the true transmission time approaches more nearly to the one or the other cannot be decided by this method.

while the galvanometer-circuit is closed by the switch, to join together the four wires of the switch at both points of interruption of the stimulating current, so as to convert them into two continuous wires. Moreover, as it is desirable not to let the individual stimulations of the nerve follow each other too rapidly, there is ample time to use each arrangement alternately, and thus to observe first the positive variation alone, then the negative with the positive following.

With the last-mentioned method of observation ('without switch') I found without exception a smaller positive variation than with the other.

A few examples will make this clear.

Cold frog. Excitation with rotation apparatus. Galvanometer tract 8 mm. Intermediate tract 37·5 mm. Duration of stimulation 20 secs.
Current of electrodes −38. Nerve current +188.

I. Stimulation with switch +21
II. " without switch $\begin{cases} -38 \\ +9 \end{cases}$
III. Stimulation with switch +13
IV. " " " +12

The positive variation of 21 which appeared with the first stimulation is the greatest I have ever seen. It was also very lasting, for 20″ after reaching the maximum, a deflection of + 10 was still shown. I did not await the complete return of the magnet in order to verify the zero point.

Warm frog. Stimulation with rotation apparatus. Galvanometer tract 7·5 mm. Intermediate tract 33 mm. Duration of stimulation 20 secs.
Current of electrodes −46. Nerve current +167.

I. Without switch $\begin{cases} -26 \\ +9 \end{cases}$
II. With switch +13
III. Without switch $\begin{cases} -22 \\ +2 \end{cases}$
IV. With switch + 6

Cold frog. Stimulation with du Bois induction-coil. Galvanometer tract 9 mm. Intermediate region about 30 mm. Duration of stimulation 10 secs.
Current of electrodes +17. Nerve current +104.

I. With switch +8
II. Without switch $\begin{cases} -13 \\ +4 \end{cases}$
III. With switch +5·5

Cold frog. Stimulation with du Bois induction-coil. Galvanometer tract 8 mm. Intermediate tract 25 mm. Duration of stimulation 12 secs.
Current of electrodes −43. Nerve current +85.

I. With switch +10
II. Without switch $\begin{cases} -19 \\ +5{\cdot}5 \end{cases}$
III. With switch + 7·5
IV. Without switch $\begin{cases} -15 \\ +3 \end{cases}$
V. With switch + 3·5

While negative variation falls off only very slightly or not at all with good nerves when moderate stimulations are frequently repeated, notwithstanding the shortness of the intervals between the individual stimulations, positive after-variation, as far as I could see, attained its maximum after the first stimulation, declining with succeeding stimulations, at first very quickly, then more slowly, and finally almost imperceptibly. In spite of very frequently repeated moderate stimulations of short duration, I never saw the positive variation quite disappear, although in comparison with the negative variation which for a long period remained unaltered, it was very small. In this statement it is assumed, however, that the nerves which demonstrate this point are healthy.

One example will suffice.

Cold frog. Both nerves used at the same time. Du Bois induction-coil. Galvanometer tract 7 mm. Intermediate tract 26 mm. Duration of stimulation 12 secs. Alternately with and without switch.

Current of electrodes +40. Nerve current +294.

	hrs.	min.	Without switch.	With switch.
I.	5	5·5		+10
II.	5	7·5	−25 + 3	
III.	5	10		+6
IV.	5	14	−22 + 2	
V.	5	17·5		+5
VI.	5	22	−20 + 1·5	
VII.	5	25		+5
VIII.	5	26·5		?
IX.	5	32·5	−19 + 0	
X.	5	34·5		+4·5
XI.	5	36·5	−20 + 0	
XII.	5	37·5		+4
XIII.	5	41	−20 + 0	
XIV.	5	43·5		+3
XV.	5	44·5	−20 + 0	
XVI.	5	46		+4
XVII.	5	49	−19 + 0	
XVIII.	5	50·5		+4
XIX.	5	52·5	−19 + 0	
XX.	5	54		?
XXI.	5	55·5		+4
XXII.	5	57	−19·5 + 0	

Positive after-variation increases up to a certain limit with increased duration of stimulation. It was already noticeable when the period of stimulation was only a fraction of a second, and after a stimulation of a second's duration it was at times considerable. The increase dependent on duration of stimulation is only conspicuous when the duration is very short, subsequently it only increases very slightly with increased duration; it falls again when duration of stimulation exceeds a certain limit, and finally with further increase quite disappears. With a stimulation which lasted for five minutes, I found in two instances after cessation of stimulation not only

no trace of positive variation, but an actual weakening of the nerve current amounting to several divisions of the scale. In this respect the positive after-effect behaves in an opposite way to the negative variation. The weakening or negative variation of the nerve current which takes place during stimulation, is constant with moderate stimulations which may last for several minutes, and increases rather than diminishes with the duration of the stimulation. With stimulations which lasted for five minutes, I repeatedly observed that there was no falling off in the amount of negative variation, but rather a moderate increase in it. This increase corresponded only in isolated cases and then only partially, with a persistent weakening of the nerve current, while in other cases the nerve-current was quite unchanged at the close of a long stimulation. The law of the dependence of the positive variation on the duration of stimulation could not be accurately deduced without the statistics of numerous experiments; because with repeated stimulation of a nerve the diminution of the positive after-variation must present itself even when the duration of stimulation remains unaltered. Immediately after a long stimulation, a short stimulation with the same strength of current gives no positive variation. If, however, the nerve has a longer period of rest, a strong positive variation again appears.

The following tables, together with those already quoted, give an approximate idea of the manner in which the amount of positive variation changes with the duration of stimulus on repeated stimulation of the same nerve. The Roman numerals again indicate the order of the individual stimulations, which followed each other at intervals of about 2–3 minutes.

Warm frog. Du Bois induction-coil. Galvanometer tract 10 mm. Intermediate tract about 30 mm. With switch.
Current of electrodes +17. Nerve current +170.

I.	Duration of stimulation	3	sec.	+2
II.	,, ,,	5	,,	+3
III.	,, ,,	10	,,	+4·5
IV.	,, ,,	20	,,	+5
V.	,, ,,	30	,,	+4
VI.	,, ,,	5	,,	+0·5

Cold frog. Du Bois induction-coil. Galvanometer tract 10 mm. Intermediate tract 35 mm. With switch. Pause between the several stimulations about 2 min.
Current of electrodes −59. Nerve current +81.

I.	Duration of stimulation	1	sec.	+1
II.	,, ,,	2	,,	?

III.	Duration of stimulation		2	sec.	+2
IV.	,,	,,	4	,,	+2·5
V.	,,	,,	8	,,	+3
VI.	,,	,,	16	,,	+3·5
VII.	,,	,,	32	,,	+3

Cold frog. Du Bois induction-coil. Galvanometer tract 9 mm. Intermediate tract about 30 mm. With switch.

Current of electrodes +40. Nerve current +134.

I.	Duration of stimulation		1	sec.	+4
II.	,,	,,	1	,,	+3
III.	,,	,,	3	,,	+4·5
IV.	,,	,,	5	,,	+6
V.	,,	,,	10	,,	+7
VI.	,,	,,	3	,,	+4·5
VII.	,,	,,	10	,,	+6·5
VIII.	,,	,,	20	,,	+6
IX.	,,	,,	1	,,	+1
X.	,,	,,	5	,,	+4
XI.	,,	,,	10	,,	+5
XII.	,,	,,	30	,,	+5
XIII.	,,	,,	5	,,	+2·5
XIV.	,,	,,	60	,,	+5·5
XV.	,,	,,	10	,,	+4

Cold frog. Stimulation with induction-coil. Galvanometer tract 9 mm. Intermediate tract about 30 mm. With switch.

Current of electrodes +17. Nerve current +103.

I.	Duration of stimulation		1	sec.	+3
II.	,,	,,	2	,,	+5·5
III.	,,	,,	5	,,	+7
IV.	,,	,,	10	,,	+8
V.	,,	,,	20	,,	+9
VI.	,,	,,	5	,,	+4
VII.	,,	,,	10	,,	+6

Cold frog. Stimulation as with preceding. With switch. Galvanometer tract 8 mm. Intermediate tract 32 mm.

First nerve.

Current of electrodes −40. Nerve current +81.

I.	Duration of stimulation		20	sec.	+6
II.	,,	,,	30	,,	+7
III.	,,	,,	40	,,	+5
IV.	,,	,,	50	,,	+4
V.	,,	,,	60	,,	+3

Second nerve.

Current of electrodes −45. Nerve current +84.

I.	Duration of stimulation		60	sec.	+10·5
II.	,,	,,	50	,,	+7
III.	,,	,,	40	,,	+5

IV.	Duration of stimulation	30	sec.	+4
V.	,, ,,	20	,,	+3
VI.	,, ,,	10	,,	+2·5
VII.	,, ,,	5	,,	+2
VIII.	,, ,,	30	,,	+3·5
IX.	,, ,,	30	,,	+3

The circumstance that it is sufficient to tetanise the nerve for a fraction of a second in order to obtain positive after-variation, suggested that even a single momentary excitation might be sufficient to produce this result to a slight extent. My attempts to demonstrate this by means of the repeating method failed from causes which we shall have to discuss in a further communication on the negative variation.

As negative variation increases with the strength of the stimulating current, so likewise does positive variation, but only up to a certain limit. In this case again more accurate data can only be arrived at from a very large number of researches. Naturally the decrease in consequence of repeated stimulation is very evident in this case, where we are dealing with increasingly stronger stimulations.

In the following series of experiments the lapse of time between two successive stimulations was about 3 minutes.

Cold frog. Du Bois induction coil. Galvanometer tract 9 mm. Intermediate tract 34 mm. With switch. Duration of stimulation 10 secs. in each case.
Current of electrodes +30. Nerve current +133.

I.	Distance apart of coils	50	cm.	+4
II.	,, ,,	40	,,	+4
III.	,, ,,	30	,,	+6
IV.	,, ,,	20	,,	+7
V.	,, ,,	15	,,	?
VI.	,, ,,	15	,,	+6
VII.	,, ,,	20	,,	+5·5
VIII.	,, ,,	30	,,	+4·5
IX.	,, ,,	40	,,	+3
X.	,, ,,	50	,,	+1
XI.	,, ,,	20	,,	$\left\{\begin{matrix}-19\\+1\end{matrix}\right\}$ without switch
XII.	,, ,,	20	,,	+5

Cold frog. Stimulation as in foregoing. Galvanometer tract 9 mm. Intermediate tract 27 mm. Duration of stimulation 10 secs. With switch.
Current of electrodes +30. Nerve current +151.

I.	Distance apart of coils	50	cm.	+0
II.	,, ,,	40	,,	+3·5
III.	,, ,,	30	,,	+5·5
IV.	,, ,,	20	,,	+7
V.	,, ,,	20	,,	$\left\{\begin{matrix}-18\\+2{\cdot}5\end{matrix}\right\}$ without switch

In order to get more accurate data of the relationship in amount between negative and positive variation, it would be necessary to make observations with two galvanometers at the same time, as already mentioned. With a stimulation of short duration, on account of the inertia of the magnet, the deflection of the needle does not correspond to the amount of negative variation : before it has reached a point in its deflection which would correspond in measurement to the decrease of the nerve current, the stimulation is already at an end. On this account all values recorded and quoted above of negative variation were far too small when the duration of stimulation was short (less than about 10 seconds). This drawback does not hold good for positive variation, because in this case one may always await the maximum deflection of the magnet. Yet even the value so found does not give a correct representation of the amount of positive variation, because this, as has been already stated, rapidly declines, and indeed in all probability too quickly for the sluggish magnet to make an excursion corresponding to the original amount of the variation. Hence it is desirable to repeat these experiments under more favourable circumstances.

The relationship in amount of positive and negative variation is best determined by experimenting with stimulations of equal strength and duration alternately with and without a switch, as has already been discussed. In this manner it was shown that the amount of positive variation not unfrequently reached half the amount of negative variation, seldom exceeded that proportion, but generally fell short of it.

The duration of positive variation under different circumstances I have not accurately determined. In cases where positive variation was considerable, minutes might pass before it fully died away. In most cases its duration is measured by seconds.

The variation of the nerve current may assume a totally different aspect if stronger induction currents be employed to tetanise the nerve, for then unipolar actions mix with them, especially if the break-shock is used. With what distance of coils and with what strength of primary current this occurs, must be specially determined for each form of experiment by special control experiments.

Du Bois-Reymond has already pointed out that, even with the most careful insulation of the circuit of the secondary coil on the one

hand, and of the multiplier- or galvanometer-circuit on the other hand, it is not possible to exclude unipolar action, especially with break-induction currents. Unless these are extremely weak, electricity flows appreciably through the intermediate tract into the galvanometer-circuit. Now, seeing that an electrical current excites a nerve especially where it enters or leaves the excitable substance of that nerve, the stimulation is no longer limited to that portion of the nerve to which the stimulating electrodes are applied, but a second direct stimulation occurs in the neighbourhood of the galvanometer electrodes. This unipolar action is greater, the greater the portion of nerve between the stimulating electrodes, and the less it is moistened. I therefore took care in my experiments that with stimulations with make and break induction currents, the intermediate tract should not be less than 25 mm., and that the stimulated tract should not be more than 5 mm.; and although numerous test experiments showed that even within these limits, when the coils were more than 13 cm. apart, unipolar action never took place, so long as the primary coil was supplied by 1 Daniell only, yet I nearly always stimulated with the coils at a distance of 20 cm. apart. If, as an exception, the coils were brought nearer together, a test experiment was always made at the end by crushing the nerve in the intermediate tract. When the stimulated tract was smaller and well-moistened, a much nearer approach of the two coils was possible without noticeable unipolar action. If the end of the nerve is not introduced into the galvanometer-circuit, but is in connection with the well-isolated muscle, and the above-mentioned conditions are fulfilled, there is not the least occasion to fear unipolar action.

The alterations in the course of the variation of the nerve current, which are brought about in consequence of the application of stronger currents and of the concomitant intermixture of unipolar action, as far as I have yet observed, are in substance the following:—

The positive after-variation is weaker, and when unipolar action becomes to a certain degree considerable, is quite lost. If unipolar action still increases, the magnet falls further short of its original deflection; or if it has been compensated, does not return to the zero point after cessation of stimulation. Hence the weakening of nerve current, which du Bois-Reymond regarded as the rule. By degrees, however, this weakening passes away, occupying several minutes in so doing if considerable, but only a few seconds if very small. Again, if excitations are repeated at short intervals

and with the same strength and duration of current, negative variation is seen to be less at each successive stimulation. The subsequent weakening of the nerve current is at the same time greater, and the impression is given of increasing exhaustion of the nerve. If the strength of current be increased by degrees, the negative variation still increases, as does at the same time the subsequent weakening of the nerve current. During stimulation with very strong currents, the nerve current disappears altogether, and it returns only partially and very slowly after stimulation has ceased. Finally, this may proceed to such an extent that the nerve current may reverse its direction during stimulation. After ceasing to stimulate, this reversed current gradually dies away; if stimulation is again repeated, the reversed current may become still stronger, and after ceasing to stimulate may continue for a period in the negative direction. At other times a lasting disappearance of nerve current ensues, the nerve appearing to lose permanently its electromotive force.

But these last-named deep-seated alterations in the electrical condition of the nerve are solely a consequence of change in the neighbourhood of the galvanometer electrodes, especially of the upper one. If the altered portion of the nerve be cut away and the electrodes be connected, one with the new section, the other with a point proportionately higher up the length of the nerve, a strong nerve current is again obtained. If now the other end of the nerve be stimulated afresh, the whole series of changes will be repeated.

It cannot therefore be supposed that this weakening or total disappearance of the nerve current depends on a corresponding decrease or total annihilation of electromotive power of the whole nerve; we are not dealing here with 'complete exhaustion of animal excitability[1].' A nerve is a relatively durable structure, and it is astonishing how long it holds out even against strong stimuli. It is only locally that it is permanently altered by strong currents. The portion which is not directly stimulated, although it may be in a condition of strong propagated excitation, suffers much less even when stimulated for a long period.

The ease with which a nerve is exhausted has been greatly overrated. If unipolar action be excluded, the nerve can be repeatedly stimulated, or stimulated for a long period, without any appreciable weakening of the nerve current or its negative variation, provided that the stimulating currents be not too strong.

[1] Compare on this point N. Wedenskii's recent communication, 'Centralblatt für die medicinische Wissenschaft' of Feb. 2, 1884.

False estimates may easily be formed of the influence of the strength of the stimulating current on the amount of negative variation, unless unipolar action be strictly excluded. Negative variation amounts only to a very small fraction of the current from transverse to longitudinal section so long as it depends solely on propagated excitation, and under these circumstances I have seldom seen it amount to a fourth part of that current. Very weak stimulations must be employed at the onset, unless it is desirable to get at once almost maximal action. That increase of the strength of the stimulating current beyond a certain very low limit has scarcely any further influence on the amount of negative variation, can naturally only be observed with methods of stimulation which exclude all unipolar action. For as soon as stimulation is started with the ordinary induction apparatus, negative variation can be made so great with moderate currents, that the whole nerve current temporarily disappears, or even changes its direction.

In his researches on negative variation, du Bois-Reymond did not exclude the unipolar actions which are occasioned by the escape of electricity into the circuit of the galvanometer. After he had convinced himself that, when tetanising a nerve with induction-currents, the electricity which flowed over and produced unipolar action did not deflect the needle, he took measures to exclude that action in special cases only. His general purpose was to show that the electromotive force of the nerve decreased during excitation. Whether this excitation was produced exclusively by stimulation of the tract between the stimulating electrodes, or whether it was produced at the same time by stimulation of the tract through which electricity was discharging itself unipolarly, appeared to him in general of no consequence, so long as the electricity led into the nerve did not influence the deflection of the needle.

In order to prove that in du Bois-Reymond's researches he did not as a rule exclude unipolar action when tetanising with induction-currents, I will quote a few passages from his 'Researches,' remarking that the words in italics are not so in the original text.

In vol. i. p. 436 [1], du Bois-Reymond says :—

'The question is whether the electricity which with this method of experiment continually spreads through the nerve, considering that the apparatus is not completely isolated, may not have an action on the needle of the multiplier. *That in this case, as in that produced by unipolar induction-contractions, electricity continually flows*

[1] Untersuchungen über thierische Elektricität.

out, is not to be doubted, for the contractions of the animal's limbs can be only very incompletely arrested by ligature of the nerve in the middle of the intermediate tract; for this ligature to be efficient it must be applied immediately above the entrance of the nerve into the muscle. With regard to the action of this outflowing of tension electricity on the needle of the multiplier we need have no anxiety.'

It only need be added to this remark, that even with the best possible insulation, unipolar action is not excluded under the above circumstances, if only the conditions already mentioned are favourable to it.

In vol. ii. p. 51, du Bois-Reymond shows proof that the negative variation of the muscle-current cannot depend on the invasion of the circuit of the multiplier by inductive electricity. For this purpose it is only necessary to ligature the nerve of the gastrocnemius between the stimulated tract and the galvanometer tract, in order to see the needle remain motionless in its place, the muscle also remaining at rest. 'Care must be taken' in using an induction apparatus of any kind for tetanising, as du Bois-Reymond observes, 'that the ligature be placed close to the point where the nerve enters the muscle. The ground for this rule lies in unipolar induction-contractions. *And if it be not adhered to, the muscle does not remain at rest, as above described, in spite of the most careful and secure ligature of the nerve;* and simultaneously with the slight tetanus which is still produced, there occurs a correspondingly small action on the needle.'

Du Bois-Reymond expresses himself in a precisely similar manner when dealing with the negative variation of the nerve current.

'Ligature and section,' he says, 'here also prevent all trace of movement of the needle. In these experiments *one must not use the induction apparatus for tetanising, on account of unipolar actions, but must employ instead a battery,* the current of which is broken and reversed at the same time by means of a Poggendorff "inversor."'

In the section which treats of the influence of various circumstances on the amount of negative variation when tetanising with reversed currents, du Bois-Reymond says (vol. ii. p. 449), 'Further, it is not unfrequently necessary to exchange the induction apparatus for Poggendorff's inversor. This is the case in the first place when the amount of negative variation in tetanisation is to be compared with the amount of the negative phase of the electrotonic state, which is itself produced by a current of equal strength with the tetanising current. . . . . In the second place, this necessity arises when one is apprehensive of disturbances of the result consequent

on the actions which occasion unipolar induction contractions. In other words, unless the whole secondary circuit, the apparatus for leading the current to the nerve, the leading off electrodes and the multiplier are completely insulated (*a state of things not easy to secure as may be well understood*) there is a continual current, now negative, now positive, according to the direction of the tetanising current flowing through the tract between the platinum plates and the pads, and through the latter and the remainder of the apparatus to the ground.' 'On the needle, indeed, this electricity has no action, but it does not fail slightly to tetanise the nerve, consequently it might show an illusory activity where there should have been none, or an exaggeration of actually existing activity. *Hence, for example, it appears that ligature or section of the nerve in the tract between platinum plates and pads does not completely arrest negative variation when induction currents are used for tetanising.*'

Du Bois-Reymond discussing, two pages farther on, the influence of the strength of the stimulating current on the amount of negative variation, says expressly, '*There is no drawback to the use of the induction apparatus in this case*' (that is to say, in comparing the actions of two currents of very different strength).

A few lines farther he remarks, 'In order to show that here likewise all depends on the density of the current and not directly on its strength, one can go to work in the manner above described for the electrotonic condition. The source of the stimulating current is left unaltered, but a collateral closure is established between the electrodes; such as a pad of blotting-paper folded several times and steeped in white of egg. It is however advisable in this case to exchange the induction coil for an inversor, *because the lessening of density no longer affects unipolar action, as it does when the source of the current itself is weakened.*' In like manner du Bois-Reymond rejects the use of the induction coil when dealing with the influence of the length of the stimulated tract, or of the influence of the distance apart of the stimulated and led off tracts.

The above is sufficient to show that in general it appeared a matter of indifference to du Bois-Reymond, whether the nerve were stimulated by induction currents exclusively in the tract between the stimulating electrodes, or whether it were stimulated in the rest of its extent at the same time. Only in particular cases, when it appeared necessary to limit the stimulation to the tract between the electrodes, did he exclude unipolar action by tetanising with battery-currents in alternately opposite directions.

It must be remembered that du Bois-Reymond was then of opinion that the electrical current excited the nerve in an equal manner throughout the whole of the tract through which it flowed. Since however Pflüger's original researches on Electrotonus, we know that the current has polar actions which are quite different at the anode from what they are at the kathode. And when du Bois-Reymond, in his researches on secondary electromotive phenomena in nerve and muscle, still maintains an equal internal (positive and negative) polarisation for the whole of the intrapolar tract, he is in my opinion in error. The so-called secondary electromotive phenomena are the consequence of polar actions, and like the excitability exhibit a polar difference. Thus it happens that electricity flowing unipolarly through the galvanometer electrodes into the circuit of the multiplier, appreciably alters the nerve in their neighbourhood, and there completely changes its electromotive behaviour; hence the alterations in the nerve current which occur during and after stimulation are in no wise solely the result of the general alteration of the nerve.

Where du Bois-Reymond discusses the influence of the strength of the stimulating current on the amount of negative variation, he says (vol. ii. p. 451) expressly: 'In this case the use of the induction-coil has no disadvantages.' And yet it is just here, where strong stimulating currents have to be dealt with, that unipolar action is most to be feared.

Thus it is sufficiently evident that du Bois-Reymond's statements differ in many respects from what we learn from the investigation of negative variation when unipolar actions are excluded. I will not here examine how far the above described behaviour of the nerve current on stimulation with strong induction currents, depends on unipolar action and thus on direct stimulation and alteration of the galvanometer tract, or how far it depends only on an increase of excitation propagated from the stimulated to the galvanometer tract. I would only add this, that with vigorous nerves and with methods of excitation which exclude unipolar actions, I never succeeded in observing such behaviour of the nerve current during stimulation as was shown when strong induction currents were used and unipolar actions in consequence obviously came into play.

I will not enter on a theoretical discussion of the positive after-variation until I have described some other electrical phenomena in stimulated nerves.

IX.

THE SO-CALLED

SECONDARY ELECTROMOTIVE PHENOMENA OF MUSCLE AND NERVE.

By L. HERMANN.

Pflüger's Archiv f. Physiologie, vol. xxxiii. p. 103.

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IX.

In a recently published treatise[1], E. du Bois-Reymond discusses the so-called secondary electromotive phenomena[2] as observed by him in muscle, nerve, and electromotive tissues, in order to give fresh support to his molecular hypothesis and his theory of electrotonus, against both of which, to my mind, fatal objections have been raised.

How important the author regards this support is seen in the opening sentences, 'I think it is now time to break the silence which I have hitherto maintained regarding certain experiments on the electromotive phenomena of tissues, with which I have been occupied nearly forty years, and to which I attach great importance,' as well as in the repeated expressions according to which all my ideas upon electrotonus had now been exploded, so that the elucidation of the subject would have to be begun anew[3].

In consideration of the heavy artillery brought against me, it will not be taken amiss if, without waiting for the further communication upon the same subject announced by the author, I go over the facts of the new position. It will then be seen to what extent the expectations and expressions of du Bois-Reymond are justified.

1. Facts observed by du Bois-Reymond.

The facts, in part new, in part previously stated, which du Bois-Reymond adduces, are briefly as follows:—

[1] 'Sitzungsberichte der Königl. Preuss.' Acad. der Wissenschaften, 1883, p. 404.

[2] Du Bois-Reymond describes as secondary electromotive such electrical phenomena as are produced by leading a current into an animal tissue, but are not detected in the tract through which the current has passed until after this is broken. He places the electromotive phenomena of animal tissues under three categories: (1) Currents inherent to the tissue at rest or in action; (2) Extrapolar effects of led-through currents during their passage; (3) Intrapolar effects of the same, i.e. the secondary electromotive phenomena. In this enumeration are omitted the extrapolar effects following the break of a current, the laws of which I first stated with regard to nerve, as du Bois-Reymond himself has mentioned. Concerning these phenomena in nerve and muscle see later.

[3] See No. VI of this Series, Sect. 15.

If a current is allowed to flow lengthwise through a tract of muscle, nerve, or electrical organ, and immediately this is broken a portion of the tract is connected with a galvanometer, ordinary internal polarisation—i. e. a current opposed to the one led through —does not always manifest itself.

Thus, if the current led into the tissue is very strong (for the thigh muscles at least that of 2 Groves, 5 Groves for the sciatic nerve) and the duration of its closure is very short, an effect appears which is in the same direction instead of in the opposite direction; or a double effect may show itself, which is first in the opposite and then in the same direction[1].

This after-effect in the same direction as the polarising current is connected more intimately with the living condition of the tissue than the one opposed to it in direction; moreover, its production is more or less clearly favoured by a direction of current which coincides with that of the natural excitation (in muscle and nerve) or of the shock (in electrical organs).

2. The Theoretical and Controversial Observations of du Bois-Reymond.

Du Bois-Reymond denotes as 'negative polarisation' the after-effect found by Peltier in a led-through tract, and which is present even with weak polarising currents, especially if these are of long duration. There is nothing to be said against this nomenclature, except that the word 'negative' is superfluous. That the phenomenon depends upon true galvanic polarisation undoubtedly follows from its whole character, from its direction as compared with that of the current which produces it, its rapid disappearance after the break of this current, the relationship of its magnitude to that of the current and to the duration of closure of the latter, and further the relationship of its amount to the position of the laminæ of heterogeneous substances in the tissues[2]; a fact discovered by myself, which du Bois-Reymond has omitted to refer to, although such an indication is of much more value than pure speculations

[1] [For convenience of description, the after-effect in the same direction as the polarising current, termed by our author 'gleichsinnig,' is denoted in this translation by the sign +, the opposed effect, termed 'gegensinnig,' by the sign −, the signs merely indicating the relation of the direction of the after-effect to that of the polarising current. Tr.]

[2] See Pflüger's 'Archiv,' vol. v. p. 232.

as to the cause of internal polarisation (du Bois-Reymond, No. VI, Sect. 21).

That galvanic polarisation is opposed to the polarising current, and thus must be, as du Bois-Reymond says, negative, is as much a physical necessity as the principle of the conservation of energy, with which in point of fact the polarisation law is in the most intimate relationship; on this account the prefix 'negative' might be done away with. But it was necessary for du Bois-Reymond, since he had arrived at the surprising idea of calling the + effect, observed by him, 'positive polarisation.' I do not find fault with the confusion which is thus produced, on the ground that for twelve years I have distinguished as positive and negative polarisation the polarisation of nerve at the positive and negative electrode; for I am not so presumptuous as to suppose that du Bois-Reymond has any regard for the technical terms introduced by myself, the discovery of which, according to him, my entire work consists of (see Sect. 21). Nor can I ground my objection on the circumstance that du Bois-Reymond once used these expressions with reference to the + and − electrodes, as Pflüger indicates in a quotation [1], as I have remarked elsewhere [2], for I cannot find the passage. It is not on this account that the term 'positive polarisation' is a surprising one, but because it represents the phenomenon as a reversal of ordinary polarisation; as if the galvanic current could produce in its circuit, instead of the customary opposing forces, forces acting in the same direction as itself, and this on a strictly comparable principle.

That du Bois-Reymond is not far from holding this very opinion, that he really holds, on the ground of his experiments, a 'reversed polarisation' as possible, follows from his whole treatise. This is evident from the circumstance that he places this side by side with the polarisation, supposed by him to be also reversed, which occurs at the limiting surfaces between salt solution and water (du Bois-Reymond, Sect. 4), or iron and zinc sulphate (Sect. 21, par. 9), quite in accordance with the scheme of true polarisation.

But if du Bois-Reymond had had the slightest doubt as to this relationship, it would have been his duty, even on the assumption that he was writing entirely for readers schooled in physics, to avoid most carefully this expression. If, on approaching a magnet to a conductor, it were observed that a current appeared in the latter which must from its direction affect the magnet pole attractively,

[1] 'Untersuchungen über die Physiologie des Elektrotonos,' p. 438.
[2] See Pflüger's 'Archiv,' vol. xxxi. p. 100.

it would certainly not be inferred with truth that under certain circumstances a reversed induction occurs in addition to the ordinary one, but it would be rather said that there must have been some error, or that the cause of the phenomenon was something wholly unconnected with induction. In like manner, if in such complicated structures as those of muscle and nerve, and with currents of from 20–50 Groves', strengths of current repudiated for other purposes, an after-effect similar in direction to the current were found to exist, no one would think of describing this effect as reversed polarisation. On the contrary, it would be said either there is some source of error, or the phenomenon has nothing to do with polarisation. Should the physics of the future indeed bring to light a reversed ('positive') polarisation, it will certainly not be by means of experiments with such damaging strengths of current, and made upon the most perishable objects in the world. The cases of iron and zinc sulphate &c. before referred to will, on closer investigation, undoubtedly show themselves to be based upon something quite different from reversal of the law of polarisation.

The author reproaches me (Sect. 15) that I have not discovered the fundamental fact of the + intrapolar after-effect (the positive polarisation of du Bois-Reymond) in a realm in which I have 'entered as a reformer;' an entirely new method, by the way, of making an attack upon irrelevant grounds. I might just as well reproach him with not having discovered the extrapolar after-effect, the law of the action current, or that of the secretion current, &c., and particularly certain phenomena of this, his own special subject, which will be brought to light in what follows. And how much more indeed might not be discovered if some one would make up his mind to go at muscle and nerve, not with the 20–50 Groves, which we have hitherto used with apprehension, but with hundreds or thousands of elements!

The most noteworthy point in the whole treatise is the manner in which the new fact of the + intrapolar after-effect is made use of. If it is true that my theory of electrotonus 'so urgently needed' for its support the electrotonus currents in muscle discovered by myself (du Bois-Reymond, Sect. 1),[1] it is still more evident that 'positive polarisation' is indispensable for du Bois-

[1] I ask myself in vain on what grounds du Bois-Reymond's theory of electrotonus less urgently needs an electrotonus of muscle than my own. The molecular scheme extends to both muscle and nerve, and what is correct for the molecules in nerve, viz. their rotation by the current, must also be right for the molecules of muscle.

Reymond's molecular theory of electrotonus. It is indeed nothing more or less than the *demonstratio ad oculos, that the current produces corresponding rotation of the electromotive molecules in the animal tissues* (Sect. 21)!

'Repeatedly,' says du Bois-Reymond (p. 223), 'and on two quite distinct hypothetical bases, Hermann has demonstrated that in the intrapolar tract a polarisation-current opposed in direction to the polarising current must prevail. I am curious to see by what auxiliary hypotheses he will deal with the polarisation current in the same direction which actually prevails.' That some of his most zealous molecular adherents, e.g. Bernstein [1] and v. Fleischl [2], have followed me and have been heretical enough to confirm the fact of an effect in the intrapolar region opposed to the current, in contradiction to himself, is a subject upon which he is silent, and he is not curious as to the auxiliary hypotheses of these authors, a circumstance which I regard as most flattering to myself.

But what is the 'positive polarisation current actually prevailing there' which my theory and my auxiliary hypotheses will have to satisfy? Since when is the proof of an after-current on opening, a ground for the assumption that the same *current existed during closure*? [3] Would physicists have ventured to deduce ordinary polarisation from the polarisation after-current alone, had not the steady decrease of the current led through, furnished a proof of the existence of the former during closure? And what would du Bois-Reymond say if some one took it into his head to conclude from the fact proved by myself and confirmed by Fick, that the anodal extrapolar region of a nerve shows on opening, an after-current opposed in direction to the polarising current, that electrotonus has also, *during closure* this direction on the anodal side?

Du Bois-Reymond observes in the intrapolar region two conflicting after-effects, one opposed to, the other in the same direction

[1] *Loc. cit.* vol. viii. p. 51.

[2] 'Sitzungsber. d. Wiener Acad. Part 3, vol. lxxvii.

[3] This absolutely incomprehensible error of transferring, without question, conditions which have been observed after opening, to the time of closure, plays the chief part in an objection raised by du Bois-Reymond against an experiment of mine (p. 200). Fifteen years ago I experimented to see if the intrapolar tract of nerve showed the large increase of current which the du Bois theory requires, and I found no trace of it. Du Bois-Reymond now thinks that this arose from my long time of closure, in consequence of which the polarisation must have been negative; with shorter times of closure positive polarisation would have given me the sought-for result. In this suggestion we have an instance of the very transference which is so unreliable.

with the current led through, the former more transitory, the latter more persistent, and, above all, observable only after short closures of very strong currents. He concludes, without any justification, that both effects are also present during closure. Now, as two simultaneous ordinary polarisations, a true ('negative') and a reversed ('positive'), are not conceivable, he assumes that the first only is due to true internal electrolytic polarisation, and that the second is due to the 'set' of the electromotive molecules in the direction of the current. He 'does not believe that any one schooled in physics will come to any other conclusion' (du Bois-Reymond, p. 222). And this and no other is the 'positive polarisation current which actually prevails,' in contrast with which I had opposed a negative; it was this which was to bring me to despair!

As to the question how this rotation of molecules is to be effected by the current, unfortunately nothing is learnt even from the new treatise. With respect to this process,' which belongs to the physics of the future, du Bois-Reymond is still unable to set up any theory. He is therefore obliged to have recourse to pulling the strings of the model of rotating molecules for the satisfaction of his credulous auditory. My request, expressed years ago, that the propounders of the molecular theory would once for all set forth an exact theory of their molecules, remains therefore unfulfilled[1]. It is characteristic that the moment an attempt is made to apply the ordinary physical modes of thought to the subject of molecules, one is repelled on the ground that the physics of the future have first to teach the necessary mode of thought[2]. My objection to the credibility of du Bois' original view according to Grothuss' theory, du Bois-Reymond appears to have acknowledged as not unfounded, but he disposes of the subject with half-intelligible evasions and with a facility which is not reassuring. He is not willing to admit electrodynamical explanations, and rightly so, as I believe. But in that case what becomes of the theory?

I can only repeat what I said ten years ago, of which I am not able to retract a word[3]. 'If the molecular schema is used for the purpose of referring the electromotive activity of the nerve cylinder to that of small particles, and definite physical actions are treated of as affecting these particles, we are compelled to demand that they should receive a more definite form which allows

[1] Pflüger's 'Archiv,' vol. viii. p. 267; vol. xx. p. 393.
[2] *Loc. cit.* vol. viii. p. 267.
[3] *Loc. cit.* vol. viii. p. 267.

of physical discussion. The original molecular theory of du Bois is quite an allowable assumption in so far as it explains the phenomena of the current of rest, (whether it is necessary is another question). The second assumption of du Bois-Reymond's, that the force of the molecules decreases during the condition of activity, is also a permissible one, for as physiological conditions produce the force of these molecules, other physiological conditions may be able to diminish it. But with his theory of electrotonus du Bois-Reymond entered another field; here, from the existence of the molecules, he drew conclusions as to the influence exercised upon them by physical processes which admit of strict definition. Immediately the question arises as to the special physical characteristics of these molecules, and it is not possible to agree with Bernstein in characterising as ridiculous either the experiments in which such physical characteristics are assumed or the objections founded upon them. If a molecule is in truth such an unapproachable thing that it is not possible to think about it in a definite physical way, then no assertion is permissible as to the effect of electrical currents upon it [1].'

The simple theory of electrotonus I have advanced, a theory founded upon proved facts, du Bois-Reymond is naturally unwilling to admit, at all events for the present, for in ten years he has not found time to make any investigations with regard to it (du Bois-Reymond, p. 201). His own position has changed in a most notable fashion. Formerly he assumed as a pure hypothesis the intrapolar rotation of molecules in the direction of the current, in order to be able to deduce from it the extrapolar effects. Now he believes that he has directly proved the intrapolar rotation (with what amount of truth has been already discussed and will be clearly explained in what follows), that he may be able to give up extrapolar electrotonus. Thus he says (p. 201), 'It is certain that even if the extrapolar electrotonic currents depend merely on diffusion of current, the nature of electrotonus as consisting in positive polarisation is not thereby affected. We should only be rid of the doubtful necessity of explaining its spread beyond the electrodes.' *The bankruptcy of the molecular hypothesis could not be more distinctly declared.* The intrapolar molecular change was originally invented merely to explain the extrapolar effects, and on its proving inade-

[1] Further remarks upon the value of the molecular hypothesis may be found in Pflüger's 'Archiv,' vol. xxvi. p. 485; to this passage I refer as being more accessible to most readers.

quate to accomplish this, became the subject of a new and unreliable assumption.

It was coolly explained as constituting the 'essence of electrotonus,' notwithstanding that I have repeatedly drawn attention to the fact that it was incapable of explaining either the contrast between an- and catelectrotonus or the indifference point. But the actually proved polarisation of the nerve-core, which does admirably explain this contrast as well as the extrapolar spread, is not the essence of electrotonus!

Excepting possibly in the case of the fanciful speculations upon the shock of the electrical fish which I have recently treated of[1] the abyss of misconception of nature by which the molecular theory is confronted has never been so appallingly displayed. Others may hold as loyal the *sacrificium intellectus* which abstains from criticising an hypothesis which claims to be sacred, I place it to my credit that I have brought back into the physiology of this department the principles which in natural science are paramount, strict thought and the rejection of error; and it is nothing to me that du Bois-Reymond, who to-day still idly talks of currents of rest of uninjured muscles, can only describe the result of my sixteen years' work (p. 402) as a 'polemic, which has brought to light more new terms than facts.'

Those however who in text-books, lectures, and popular writings blindly go on spreading statements and hypotheses which have been refuted, will by so doing place themselves in a position of which one day they will be ashamed.

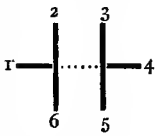
3. Investigation of the intrapolar after-currents of Muscles and Nerves.

We now enter upon the task of investigating the + after-effect discovered by du Bois-Reymond, in a way which may guide us to its elucidation. I repeated du Bois-Reymond's chief experiment so as to obtain an idea of the phenomenon in question; it then appeared desirable to modify in one respect his method. He placed the leading-in electrodes on one lateral surface of the muscle, the leading-off ones on the other. Under certain assumptions a

[1] *Loc. cit.* vol. xxvi. p. 483.

+ after-effect might be caused by ordinary polarisation with this arrangement, supposing, for instance, enveloping layers of badly-conducting polarised portions of tissue to be present. Should the + after-current also appear by leading-off on the same surface with the leading-in electrodes, then this possibility is removed. As a matter of fact this is the case: no marked difference appears between the results obtained with contacts on the same and on opposite surfaces.

The simplest arrangements sufficed to show the phenomenon. A Pohl's commutator without cross-wires served to close the galvanometer-circuit immediately after the battery-circuit was opened, the commutator being coupled up by 1, 2 with the battery, by 4, 5 with the galvanometer-circuit. In my former experiments upon extrapolar after-currents[1] this method was not satisfactory, owing to insufficiency of insulation; but the effects of insufficient insulation are much less marked in the case of intrapolar than in that of xtrapolar after-currents. Subsequently the wooden reverser was replaced by a paraffin one. The switching from battery to galvanometer-circuits was effected as quickly as possible by hand, in the case of long closures by a clock.



In muscle, after a very short closure, the after-current appeared to be mostly diphasic[2]; a quick, sometimes momentary — being followed by a long-enduring + deflection which mostly only

[1] 'Untersuchungen zur Physiologie der Muskeln und Nerven,' Part 3, Berlin, 1868, p. 71.

[2] It seems to me that du Bois-Reymond has seen this diphasic (*doppelsinnig*) effect more seldom than I have, and the cause probably lies in the extreme lightness of the magnet system of my galvanometer; it weighs only 0·9 gr. (see 'Pflüg. Archiv,' vol. xxi. p. 436). Besides this, very effectual damping gives aperiodicity with a relatively slight amount of astasia: it is thus conceivable that a heavier or more astatic system may not show the very small negative jerk of which my instrument gives plain indications.

It may also be noticed here that with rapidly vanishing polarisation-currents the velocity of the movement of the magnet must largely influence the amount of the deflection, since the current itself becomes smaller during the deflection. This influence, as to which I have many times convinced myself, is rendered especially predominant through aperiodicity. On this ground, as I have often seen, the deflections caused by rapidly decreasing polarisation-currents are not diminished by withdrawal of the bobbin to the same extent as in the case of constant currents; the shorter time which the diminished deflection requires enables the maximum of deflection to coincide with a greater strength of current than would be the case if the instrument were rendered more sensitive.

incompletely disappeared. I can entirely verify the fact that the appearance of the + after-current, and of this only, is favoured by short times of closure and by strong currents; that, further, the phenomenon is intimately connected with the vitality and, as I am able to show, with the excitability of the animal-tissue. By fatigue, even when produced by an ordinary tetanus, + after-currents become diphasic, and diphasic ones become entirely −. On the other hand, the − after-current, especially in a nerve, is a phenomenon which, even in summer, can be demonstrated for from 24 to 48 hours, feebly indeed, but quite plainly; whilst the + after-current appears always with fresh preparations, and these alone. As boiling-water, according to du Bois-Reymond, confirmed by myself, puts an end also to the − after-current, possibly the most correct expression of the facts would be this, *the − after-current is associated with the maintenance of structure, the + with that of life.* Electrotonus has a certain resemblance to the − after-effect, inasmuch as it often shows plainly traces of its presence in exhausted and long-kept nerves.

If then the + after-effect is thus intimately connected with excitability, the first question which arises is, whether it may not possibly be itself an excitation phenomenon. It is inconceivable to me how du Bois-Reymond could have overlooked this, and so given himself the trouble of seeking an explanation in the physics of the future.

My first thought on reading du Bois-Reymond's communication was that this + after-effect was the current of action proceeding from a prolonged break-excitation. It is well known, as Pflüger discovered, that both in nerve and muscle the break of a strong current is followed in the anelectrotonic tract by a violent and prolonged excitation. We may fairly assume that this excitation is strongest and most prolonged at the anode itself, and decreases towards the indifference point. According to the laws of action-currents which I have advanced, a point near the anode must, after break, be negative to one further off, and thus an intrapolar after-current must be produced having the same direction as the polarising-current; as, according to Pflüger, the indifference-point when strong currents are used lies close to the kathode (at least in nerve), this condition must spread throughout the entire intrapolar region.

This current is so directly necessary, and without being connected with any theory is in itself so undoubted, that du Bois-

Reymond must have thought of it, and he was then bound to investigate to what extent it was connected with the phenomenon discovered by himself, even if there had been some reasons for assuming that it was not by itself a sufficient explanation of the facts; but, as will be seen, such reasons are not forthcoming. Instead of this, such an explanation is not once mentioned, simply because the molecular theory has again asserted its power of paralysing the next step forwards.

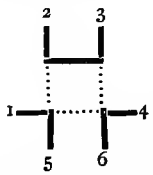
Let us next see how the indications of this action-current should present themselves. When the indifference-point is in the middle, then, after break, the anodic half of the intrapolar region, if appropriately led off, would show an action-current in the same direction as the polarising current; this must also be the case when one leading-off electrode is in the kathodic, the other in the anodic half; on the other hand, if both leading-off electrodes were situated in the kathodic half, the current would be absent; but it is conceivable that, owing to electrotonic spread of the anodic action-current, it might be present even in this last case. With strong currents the + after-current should be found throughout the intrapolar region.

This current thus comes in conflict with Peltier's — polarisation after-current in the intrapolar region. But it is essential to polarisation after-currents, first that they become stronger, the longer within certain limits the polarising current has been closed; and, secondly, that they rapidly decrease after the break of the latter. The most favourable condition for the development of the action-current ('positive polarisation' of du Bois) is above all very short closure of polarising current, so that the maximum of polarisation is not obtained with such closure; but even under such conditions, during the first moment after break, the polarisation — effect is stronger than the + action-current, and the after-current is therefore diphasic. The chief facts can be thus thoroughly and simply explained without taking into account certain new phenomena to be presently referred to.

The next step, necessary to prove the validity of this explanation, is to investigate the influence which the position in the intrapolar region of the leading-off electrodes exerts on both — and + after-effects; a problem which du Bois-Reymond has not investigated.

Two pairs of leading-off electrodes were brought into contact with the intrapolar region, and each pair connected with the circuit of a separate galvanometer and compensator.

Herr A. von Gendre of St. Petersburg undertook to read one of the galvanometers. The two galvanometer-circuits were closed at the same moment by means of a commutator, arranged so that one was connected with 1 and 6, the other with 4 and 5. The commutator had a paraffin bed instead of the ordinary wooden one, this excellent insulating material being readily workable on the lathe. The two cups 2 and 3 were in the battery-circuit, and on the commutator being turned to that side were connected by means of a copper arc. The connections between the three copper arcs, indicated in the figure by dotted lines, were of paraffin. Further, the battery, of from 1–18 zinc carbon elements, stood upon paraffin feet.

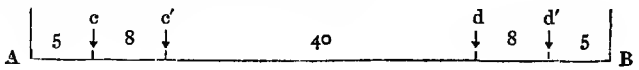


For the experiments on nerve, as a rule two sciatics were used, joined together in such a way that the central end of one lay in connection with the peripheral end of the other. This was in order to eliminate as completely as possible the difference in the behaviour of nerve, stated by du Bois-Reymond to depend on the centrifugal or centripetal direction of a current. For the experiments on muscle, the groups of gracilis and semimembranosus were used, the left and right groups being left in their natural attachments to the symphysis; and hooks fastened to ivory pegs by silk thread were attached to the muscle groups and immovably extended them.

The leading-in contacts were at the two knee ends respectively, and the two pairs of leading-off electrodes were brought as close as possible to these, each pair being thus in connection with the lower division of a muscle group, so that du Bois-Reymond's asserted difference in the behaviour of the upper and lower part of the muscle might be eliminated from the experiment.

With nerve there occurred no marked difference in the deflections of the two led-off regions attributable to the direction of the polarising current; that is to say, it made no difference as regards the after-current whether the led-off region lay in the neighbourhood of the anode or in that of the kathode.

Example. Two sciatic nerves placed together in the manner before described. The schema indicates the position of the electrodes (the leading-off electrodes are marked thus ↓).



The numbers denote the intervals in millimeters—polarising current led in at A–B, leading-off electrodes at cc′ and dd′.

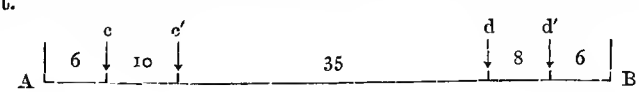
The battery elements, as in all the following examples, were zinc and carbon, the duration of closure, unless otherwise stated, being extremely short. As no special care was taken to make the closure always of equal length—this being effected by the hand—the inequality in the deflections of successive experiments may be taken as due to this. Comparisons of the amounts of deflection can only therefore be made in the case of observations taken at the same time in cc′ and in dd′. This holds good for all the following experiments.

The comparison of the two deflections in cc′ and dd′ is naturally further complicated through differences in the two galvanometers—differences as well in the delicacy as in the period of oscillation of the magnets. We have taken the necessary readings for correcting the deflections so as to give them the value which they would have had if the two instruments had been identical. But this reduction has no practical importance, and is therefore omitted in the experiments given. The first glance shows that the galvanometer in connection with cc′ was the more delicate one. A deflection off the scale is denoted thus ∞.

Number of cells.	Direction of polarising current.	After-current deflection.	
		In cc′.	In dd′.
3	←	− 75 C	− 30 A
,,	←	− 32 C	− 20 A
,,	→	−158 A	− 80 C
,,	→	−102 A	− 40 C
9	←	− 88 } C + 43 }	− 55 } A + 25 }
,,	←	− 98 } C + 30 }	− 40 } A + 20 }
,,	→	−198 } A + 38 }	− 55 } C + 35 }
,,	→	−115 } A + 30 }	− 50 } C + 40 }
18	←	−215 } C + 95 }	− 55 } A + 65 }
,,	→	− ∞ } A +100 }	−280 } C + 80 }

The letters A and C denote that the leading-off electrodes lay respectively in the neighbourhood of the anode and kathode.

Another example. Two sciatic nerves, as in the preceding experiment.



Number of cells.	Direction and duration of closure of polarising current.	After-current deflection.	
		In cc'.	In dd'.
3	⟵ short	−167 C	− 40 A
,,	⟵ ,,	−138 C	− 34 A
,,	⟶ ,,	− 46 A	− 15 C
,,	⟶ very short	−210 A	− 70 C
9	⟵ short	− ∞ } C + 47 }	−164 } A + 11 }
,,	⟵ ,,	−498 } C + 41 }	−140 } A + 10 }
,,	⟶ ,,	−216 } A + 17 }	− 40 } C + 35 }
,,	⟶ ,,	−500 } A + 10 }	−105 } C + 20 }
18	⟵ very short	−343 } C +153 }	− 40 } A + 65 }
,,	⟵ ,, ,,	− ∞ } C +132 }	−313 } A + 39 }
,,	⟵ longer	− ∞ } C +124 }	−266 } A + 35 }
,,	⟶ short	−463 } A + 97 }	− 67 } C + 60 }
,,	⟶ longer	− ∞ } A + 42 }	−161 } C + 60 }

Quite otherwise is the case in muscle. In many experiments the + after-current was so decidedly favoured by the neighbourhood of the anode as to leave no question of chance: that is to say, the + phase was, both absolutely and relatively to the − phase, markedly stronger in the led-off region near the entry of the polarising current than in the other regions; and by certain strengths of polarising current it was generally only found in this region. As this relation remained constant with reversal of current, its cause could not be special to the muscle group investigated. (The direction of the current was generally changed after two experiments.) Although the majority of experiments showed the above relations, there were some dubious ones; some in which nothing of the kind was observed, and some which appeared to give opposite results. But one single exception is sufficient to invalidate a law, however distinctly the majority of experiments may indicate it.

In this embarrassment a circumstance happily came to my mind which has very often been overlooked, namely, the *inscriptio tendinea* with which, as is well known, the gracilis and semimembranosus of

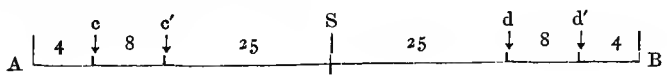
the frog are provided[1]. If a current is led through the entire length of the muscle, then clearly each fibre has an anodic and a kathodic region where it is broken by the *inscriptio*. Supposing one led-off region to lie in the lower half of a gracilis through which an ascending current passes, and to be symmetrically placed between *inscriptio* and the muscle end; then it is by no means, as might be thought, in the anodic region, but exactly midway between an anode and a kathode. That, in spite of this, the gracilis and semimembranosus show for the most part the beforementioned relations may be due, first, to the oblique direction of their *inscriptiones*, a truly symmetrical position of leading-off contacts between these and the lower ends of the muscles not being possible; secondly, to the fact that the *inscriptio* does not completely traverse the semimembranosus[2]; and thirdly, to the close proximity (as close as possible) of the led-off region to the lower end of the muscle.

In any case, as the *inscriptio* must tend to obscure any law, it was advisable to pass on to other muscles, and I chose the sartorius. This rewarded investigation by bringing out, without exception and in the most forcible manner, the following simple law:—

In muscle the + phase either, as is generally the case, appears only in the led-off portion near the anode; or, if it comes into view in the kathodic region (which is the case when strong currents are used), is incomparably weaker than in the anodic.

The — (first) phase, on the other hand, is stronger in the kathodic region; but this difference is much less marked, and can be explained by the fact that the strong development of the + effect must necessarily prevent the complete accomplishment of the — deflection.

Example. Two sartorius muscles, both attached to the symphysis S. Current led in at the knee-ends A and B. Leading-off contacts in the neighbourhood of the knee-ends at cc′ and dd′. The following schema gives the intervals:—



[1] See Pflüger's 'Archiv,' vol. x. p. 49; vol. xv. p. 223.

[2] See du Bois-Reymond, 'Archiv für Anat. u. Physiol.' 1876, p. 351 (Ges. Abh. ii. p. 573).

Number of cells.	Direction of current.	After-current deflection.	
		In cc′.	In dd′.
1	←—	− 10 c, C	− 16 a, A
,,	—→	− 5 a, A	− 13 c, C
3	←—	− 20 c, C	− 12 + 100 a, A
,,	—→	− 45 + 45 a	− 107 k, K
,,	←—	− 53 c, C	− 37 + 100 a, A
,,	—→	− 31 + 45 a, A	− 76 c, C
9	←—	− 140 c, C	− 26 + 524 a, A
,,	—→	− 80 + 202 a	− 290 c, C
,,	←—	− 159 + 6 c, C	− 87 + 410 a, A
,,	—→	− 120 + 130 a, A	− 102 + 32 c, C
18	←—	− 357 + 36 c, C	− 202 + 578 a, A
,,	—→	− 243 + 177 a, A	− 558 + 48 c, C

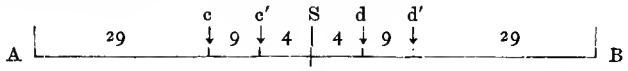
The readings in cc′ were taken by Herr v. Gendre, those in dd′ by myself. The delicacy of the two galvanometers was nearly equal; mine was a little the more delicate. That the deflections in spite of this were relatively smaller in cc′ than in dd′ was due to the slower swing of the magnet of the first galvanometer, so that during the deflection the after-current had already markedly decreased; this we ascertained by special experiments[1].

In order to establish the law still more firmly, experiments were now arranged in which the two sartorius muscles were led off at the upper end in the neighbourhood of the symphysis. If the law holds good, then the + phase should appear more easily or even alone in that muscle to which the kathode is applied (i. e. the reverse of what was previously the case), since now the leading-off contacts, though on the kathodic muscle, are in the neighbourhood of the physiological anode. The prediction was most beautifully fulfilled.

[1] The galvanometer used in cc′ was an ordinary Wiedemann, that in dd′ one constructed by myself and described in Pflüger's 'Archiv,' vol. xxi. p. 430. The damping arrangement allows aperiodicity with relatively small astasia; hence its superiority as mentioned before in the text.

In the tables the letters a and c indicate that the deflection to the record of which they are appended belongs to the muscle to which the anode and kathode are respectively applied. The capital letters A and C indicate that the region led off was in the neighbourhood of the physiological anode and kathode respectively. In the preceding experiments the physiological and actual anodes and kathodes were identical. This is not the case in the following ones.

Example. Sartorius muscles attached to the symphysis. Leading-in electrodes at the two knee-ends A and B. Both muscles led off in the neighbourhood of the symphysis at cc′ and dd′. The schema gives the intervals—



Number of cells.	Direction of current.	After-current deflection.	
		In cc′.	In dd′.
1	←—	− 20 c, A	− 15 a, C
,,	—→	− 15 a, C	− 53 c, A
3	←—	− 54 / + 26 } c, A	− 119 a, C
,,	—→	− 24 a, C	− 50 / + 34 } c, A
,,	←—	− 99 / + 13 } c, A	− 97 a, C
,,	—→	− 26 a, C	− 68 / + 23 } c, A
9	←—	− 43 / + 35 } c, A	− 134 a, C
,,	—→	− 69 a, C	− 28 / + 361 } c, A
,,	←—	− 62 / + 30 } c, A	− 191 a, C
,,	—→	− 88 a, C	− 38 / + 393 } c, A
18	←—	− 83 / + 45 } c, A	− 269 a, C
,,	—→	− 186 a, C	− 106 / + 408 } c, A
,,	←—	− 53 / + 45 } c, A	− 188 a, C
,,	—→	− 220 a, C	− 222 / + 302 } c, A

The galvanometers used were the same as in the previous experiments, and, as is evident, the remarks as to the differences between their deflections apply here. (The readings in cc′ were taken by Herr v. Gendre with the Wiedemann, those in dd′ by myself with my galvanometer.)

The striking result of this set of observations made me think that the different influence of the anode and kathode respectively might be more markedly obtained by uniting one of the leading-off electrodes with the anode or the kathode of the polarising current. This method, if literally carried out, would involve the danger of bringing in external polarisation (in the electrode itself), but naturally it is only necessary to make the physiological electrodes identical, i. e. the points of connection of the battery and of the galvanometer with the muscle fibres; and to do this I proceeded as follows.

A gastrocnemius was stretched out by means of my extension arrangement, and a polarising current led in at the Achilles tendon and the knee-end. One of the leading-off electrodes was also placed on the Achilles tendon somewhat above the leading-in electrode, the other lay on the surface of the muscle at about the junction of the lower and middle thirds of the fleshy part. It is evident that with an ascending current the lower ends of the muscle fibres constitute the physiological anode and that it is here that the lower leading-off electrode is in contact with the muscle substance, whilst the upper leading-off contact lies far removed from the physiological kathode; with a descending current the physiological kathode and lower leading-off contact are identified.

The expected result was most beautifully brought out. With descending currents, — deflections only were almost always obtained; with ascending currents, diphasic (− +) deflections or + alone. Moreover, now even with one zinc-carbon cell the + phase showed itself; whereas with the ordinary method at least two or three cells were needed. It may therefore be stated that leading-off at the anode itself is the most favourable, at the kathode itself the least favourable condition for obtaining the + intrapolar after-effect.

Example 1. (Left hand.) Gastrocnemius led in and off as just described. Current of rest ↑ 318 scale = 0·0033 D. (In the course of the experiment the current of rest due to the summing up of the residual + phases with ascending polarising currents increased to five times this amount; this increase showed itself in all the experiments.)

Example 2. (Right hand.) Gastrocnemius as above. Current of rest ↑ 32 (delicacy diminished) = 0·0065 D. (Increased during experiment to $4\frac{1}{2}$ times as much.)

Example 1.			Example 2.		
Number of cells.	Direction of current.	Deflection (lower end of muscle).	Number of cells.	Direction of current.	Deflection (lower end of muscle).
1	↓	−167 c	Delicacy of galvanometer considerably decreased.		
,,	↑	− 35 / +122 a	1	↓	− 13 c
,,	↓	−290 c	,,	↑	− 8 / + 7 a
,,	↑	−132 / +127 a	,,	↓	− 25 c
,,	↓	−154 c	,,	↑	− 15 / + 3 a
,,	↑	− 89 / +125 a	3	↓	− 47 c
3	↓	−320 c	,,	↑	− 19 / + 50 a
,,	↑	− 45 / + ∞ a	,,	↓	− 51 c
Delicacy of galvanometer greatly decreased.			,,	↑	− 13 / + 44 a
,,	↓	− 6 c	9	↓	− 38 c
,,	↑	− 1 / + 15 a	,,	↑	+123 a
,,	↓	− 22 c	,,	↓	− 27 c
,,	↑	− 1 / + 18 a	,,	↑	−110 / + 81 a
6	↓	− 13 c	18	↓	−237 c
,,	↑	− 24 / + 31 a	,,	↑	− 40 / +107 a
9	↓	− 9 c	,,	↓	− 85 / + 19 c
,,	↑	− 17 / + 32 a	,,	↑	− 30 / + 58 a
Delicacy of galvanometer slightly increased.					
,,	↓	− 41 c			
,,	↑	−147 / + 93 a			
,,	↓	− 63 c			
,,	↑	−127 / + 43 a			

There is another method by which the physiological electrode of a polarising current can be identified with the physiological leading-off contact, namely, leading a polarising current into a piece of dead muscle, and leading-off to a galvanometer from this in place of the tendon in the experiment just described. The employment of this method did not give those results which might at first sight have

been expected, but, on the contrary gave to a certain extent opposite ones; these however confirmed our main law in a most striking and instructive way.

For these experiments I made use of a method of my own for causing heat rigor in a tract of muscle[1]; which du Bois-Reymond has more recently described as the production of a 'thermal cross-section[2].' The experiment naturally allowed the use of a single muscle arranged as in the schema of that just described, a tract in heat rigor taking the place of the tendon. The following arrangement was however still better adapted for this experiment.

The two sartorius muscles were so prepared that they remained attached to the symphysis. They were then placed together, and the symphysis with the muscle attachments was dipped 8 mm. deep into hot water; heat rigor being thus produced. The muscles were then drawn apart and stretched out by fixing the knee-ends with hedgehog spines to a cork board. The polarising current was led in at the knee-ends, the leading-off contacts were placed, one in the region of heat rigor (at the symphysis), the other on the unimpaired surface of the same muscle in its upper half. If the right muscle be thus led off, then the left one serves merely as an indifferent conductor of the polarising current; the muscle experimented upon is however the right one, in which the upper polarising and upper leading-off electrodes are identified and lie on the thermal cross-section. At the end of an experiment the other muscle may be used by shifting the leading-off electrodes. The full demarcation current is naturally led off and has to be compensated.

The preceding experiments would lead us to expect that the + phase of the after-current should only occur when the physiological anode is united with one leading-off contact, or, in other words, when the polarising current is directed from the muscle not led off to the led-off one; and hence is in this 'abterminal.' Instead of this, the + phase never appeared under such circumstances; but sometimes appeared with the polarising current directed the opposite way.

The cause of this apparent discrepancy was clear to me. It is known that Biedermann found that the breaking excitation failed in the case

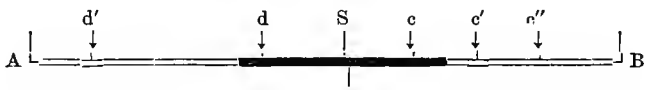
[1] See Pflüger's 'Archiv,' vol. iv. p. 167.

[2] 'Archiv f. Anat. u. Physiolog.' 1873, p. 526 (Ges. Abh. ii. p. 409).

of currents whose anode coincided with an artificial cross-section. *The failure of the + phase of the after-current with a polarising current directed from dead to living tissue, is therefore a new and striking proof that this after-current is connected in the most intimate manner with the breaking excitation.* I may remark here incidentally, that these experiments offer many opportunities for verifying the statements of Biedermann and Engelmann (with van Loon) as to the excitatory effects of currents directed respectively from dead to living and from living to dead tissues, since there are here two muscles in the circuit, in one of which the current is in the first direction 'abmortal,' in the other or second direction 'admortal[1].'

It has already been noted that the + phase sometimes appeared with atterminal direction of current. As might be readily predicted, its appearance was more marked the nearer to the knee end the leading-off electrode was placed; the farther therefore, with living to dead direction of current, this electrode was moved into the region of anelectrotonus.

Examples. Each experiment was made upon two sartorius muscles arranged and led off in the manner just described. The following schema shows the arrangement:—



The symphysis is marked S as before. AS, BS are the two sartorii; the shaded parts indicate the portions of the two muscles in heat rigor. The electrodes of the polarising current are at A and B; and the positions of the pairs of leading-off electrodes in the several experiments are indicated by cc′, cc″, dd′.

[1] The nomenclature, as bearing upon the direction of a current with reference to the ends of the fibres ('Archiv,' vol. xvi. p. 193), is an adaptation of that used by Biedermann, Engelmann, Grützner, and others; these writers describe as abterminal a current directed from the ends of the fibres into the muscle when the end of the fibre is an artificial cross-section; such currents I term 'abmortal.' Biedermann's facts make such a distinction desirable. For instance, I can thus shortly express my results—an abterminal current gives under certain conditions a + after-current phase, an abmortal does not. [In the text the terms 'abmortal' and 'admortal' used by Hermann are translated 'dead to living,' 'living to dead.' Tr.]

Example 1.			Example 2.		
Number of cells.	Direction of current in A B.	After-current deflection.	Number of cells.	Direction of current in A B.	After-current deflection.
Led off at cc′, current of rest → ∞ =0·0311 D.			Led off at cc″, current of rest → ∞ =0·0465 D.		
1	←	− 26 living to dead	1	←	− 41 living to dead
,,	→	− 32 dead to living	,,	→	− 40 dead to living
3	←	− 64 l. to d.	3	←	+ 30 l. to d.
,,	→	− 42 d. to l.	,,	→	−160 d. to l.
6	←	− 42 l. to d.	6	←	−153 + 98 } l. to d.
,,	→	− 61 d. to l.	,,	→	−260 d. to l.
9	←	− 1 + 26 } l. to d.	9	←	−130 +232 } l. to d.
,,	→	− 60 d. to l.	,,	→	−630 d. to l.
18	←	−370 +110 } l. to d.	18	←	−230 +659 } l. to d.
,,	→	−590 d. to l.	,,	→	−∞ d. to l.

Number of cells.	Direction of current in A B.	After-current deflection.	Number of cells.	Direction of current in A B.	After-current deflection.
Led off at dd′, current of rest ← 565 scale = 0·0436 D.			Led off at dd′, current of rest ← ∞ =0·0448 D.		
1	←	− 20 dead to living	1	←	− 70 dead to living
,,	→	− 10 l. to d.	,,	→	−117 + 30 } l. to d.
6	←	−315 d. to l.	,,	←	− 30 d to l.
,,	→	−482 + 55 } l. to d.	,,	→	− 53 + 14 } l. to d.
9	←	−429 + 10 } d. to l.	4	←	−183 d. to l.
,,	→	−215 +108 } l. to d.	,,	→	− 45 + 55 } l. to d.
18	←	− ∞ d. to l.	9	←	−496 d. to l.
,,	→	− ∞ +118 } l. to d.	,,	→	−516 +258 } l. to d.
			18	←	− ∞ d. to l.
			,,	→	− ∞ + ∞ } l. to d.

The striking result of this experiment led to a method by which the different effects dependent upon direction of current were still more markedly shown. It is seen above that (at least within the limits of current strength there employed) currents directed from dead to living tissue hardly ever give the + phase, which only appeared with a current directed from living to dead tissue, the arrangement being that one leading-in and one leading-off electrode lie in the region of artificial cross-section; further, that with currents directed from living to dead tissue the appearance of the + phase is favoured by the proximity to the anode of the electrode leading off the living tissue. Could this latter be identified with the anode, the conditions for the production of the phenomena would be the most favourable.

This is obtained in the gastrocnemius, for instance, when a thermal cross-section is made in the upper end by dipping it into hot water. Upon this one leading-off and one polarising electrode are placed, and then the other leading-off and the other polarising electrode are placed upon the Achilles tendon; both places offer sufficient room for two kaolin points. With this arrangement the descending (dead to living) current never gives the + phase; on the other hand, the ascending (living to dead) current gives it even when quite weak. The state of things is evidently this; the leading off occurs quite at the anode and kathode, independently of the direction of the current. The anode, however, in the case of a descending current, lies upon the artificial cross-section; accordingly it is only with ascending currents that the + phase is produced.

But it is possible to go still farther. So far the union of a leading-in and a leading-off electrode has been effected by a part of the muscle which acts as an indifferent conductor, whether this be the tendon or a portion of tissue in heat rigor. There is however no objection to effecting this by a piece of electrode kaolin. This is indeed capable of internal polarisation according to du Bois-Reymond, but only 'negatively;' and at any rate it can scarcely be more polarisable than a piece of tendon or dead muscle.

When it is desired to lead off from the entire portion of tissue through which the polarising current passes, a very simple arrangement is the following; the kaolin points of the leading-off electrodes are laid upon the tissue, and upon these points are placed those of the polarising electrodes. The 'external' polarisation

which prevented du Bois-Reymond (p. 348) from using polarising as leading-off electrodes is in this way completely avoided[1].

When one such double electrode lies upon a living, the other upon a dead portion of muscle, then, as might be expected, the + after-current only appears following such currents as are directed from the former to the latter, i.e. from living to dead tissue. In every way the above arrangement presents itself as the most favourable one for obtaining the + after-effect of muscle, even when both double electrodes lie upon living tissue, since in all cases the leading-off is from the most effective portion of the anodal intrapolar region.

Examples. Sartorius muscle, with one end *A* in heat-rigor. Leading in and off by means of double electrodes at cc′.

Example 1. *Example* 2.

Number of cells.	Direction of current.	After-effect. Actual reading.	After-effect. Calculated reading with most delicate position.
Current of rest → ∞ = 0·0189 D. One coil only used ($\frac{4}{5}$)[2].			
1	←	−267 + 35	−334 + 44 living to dead
,,	→	−298	−372 dead to living
Coil farther away ($\frac{1}{20}$).			
4	←	− 72 + 40	−1440 + 800 l. to d.
,,	→	−110	−2200 d. to l.
9	←	−272 + 28	−5440 + 560 l. to d.
,,	→	−400	−8000 d. to l.
18	←	−299 + 21	−5980 + 420 l. to d.
,,	→	−630	−12600 d. to l.

Number of cells.	Direction of current.	After-effect. Actual reading.	After-effect. Calculated reading with most delicate position.
Current of rest ← ∞ = 0·0386 D. Full delicacy of galvanometer.			
1	←	−426 + 105	−426 + 105 living to dead
,,	→	−343	−343 dead to living
Coil farther away ($\frac{1}{20}$).			
4	←	−190 + 20	−3800 + 400 l. to d.
,,	→	−190	−3800 d. to l.
9	←	−312 + 55	−6240 + 1100 l. to d.
,,	→	−179	−3580 d. to l.
Coil still farther away ($\frac{1}{60}$).			
18	←	− 89 + 17	−5340 + 1020 l. to d.
,,	→	−142	−8520 d. to l.

[1] In this, as in all experiments of this nature, if a rheochord be used in order to obtain weak polarising currents, the break must lie between the tissue and the rheochord, not between the latter and the battery. (See Pflüger's 'Archiv,' vol. vi. p. 318.)

[2] The fractions in the brackets indicate the relative delicacy in each particular

There is then abundance of proof of the fact overlooked by du Bois-Reymond *that the + phase of the after-current in muscle prevails only in the region of the anode.*

In the case of nerve the experiments which have been previously cited showed that there was no difference of behaviour whether the leading-off occurred close to the anode or close to the kathode. This should not surprise us since, in nerve, anelectrotonus extends with strong currents quite up to the kathode. In spite of this it seemed desirable to employ upon nerves, the methods used in the case of muscle in order to obtain more decided differences between the behaviour of nerve at the anode and kathode: in point of fact such differences were obtained.

For this purpose a polarising and a leading-off electrode were laid upon a destroyed spot in a nerve. The middle portion of a nerve preparation, made as before described by laying two nerves together, was destroyed by dipping it into hot water (the preparation being first folded in the middle so that the two halves lay side by side). As however the vapour severely injures the remaining portions of the preparation, as described by me in an earlier work; this method was abandoned[1], and in the later experiments the piece of nerve-preparation was effectually squeezed between the blades of a small vice. Still, the first method of treatment gave results invariably like the second.

It appeared that in nerve also, with appropriate strength of current, the + phase of the after-current regularly failed when the physiological anode and one leading-off electrode lay on the artificial cross-section.

Example. Two sciatic nerves placed side by side in opposite directions; and squeezed in the middle for 9 mm. (the squeezed part is indicated in the schema by the dark line). Polarising-current led in at AB.

case (due to particular distance as well as length of coil), the highest attainable delicacy being taken as unit. The distances were so arranged that this ratio should be as nearly as possible a round number. With my galvanometer, the bobbin of which is immovable, another extra bobbin was used. See Pflüger's 'Archiv,' vol. xxiv. p. 254.

[1] *Loc. cit.* vol. xxiv. p. 254.

Led off at cc′.			Led off at cc″.		
Number of cells.	Direction of polarising current.	After-current.	Number of cells.	Direction of polarising current.	After-current.
Current of rest → 437 scale = 0·0149 D.			Current of rest ← 394 scale = 0·0099 D.		
1	←	− 34 living to dead	1	←	− 97 dead to living
,,	→	− 32 dead to living	,,	→	− 74 living to dead
4	←	−118 l. to d.	4	←	−210 d. to l.
,,	→	−121 d. to l.	,,	→	−200 l. to d.
9	←	−132 / + 58 l. to d.	9	←	−202 d. to l.
,,	→	−206 d. to l.	,,	→	−550 l. to d.
			Half the coil used ($\frac{4}{5}$).		
18	←	−∞ / +82 l. to d.	18	←	−433 d. to l. (−541)
,,	→	−552 d. to l.	,,	→	−587 / + 15 l. to d. (−734 / + 19)
			,,	←	−395 d. to l. (−494)
			,,	→	−580 / + 18 l. to d. (−725 / + 23)

As in the last-mentioned experiments on muscle, the two pairs of electrodes were now identified, and the one united pair was placed upon a destroyed spot, the other upon a living portion of a nerve-preparation.

In this case also, with a few exceptions in which very strong currents were used, the + after-effect appeared only with polarising-currents directed from living to dead tissue, and on account of the favourable leading-off it revealed itself after a weak current such as that of one zinc carbon cell.

Example. Two sciatic nerves placed together as before and crushed at one end (dark line in schema) united leading-in and leading-off electrodes at CC′.

Number of cells.	Direction of polarising current.	After-current.	
		Actual readings.	Calculated for greater delicacy.
Current of rest → 334 scale = 0·01 D.			
1	←	−165 }	−165 } living to dead
		+ 23 }	+ 23 }
,,	→	−202	−202 dead to living
4	←	− ∞ }	− ∞ } living to dead
		+49 }	+ 49 }
,,	→	− ∞	− ∞ dead to living
Half the coil used ($\frac{1}{2}$).			
,,	→	−106 }	−133 } living to dead
		+ 24 }	+ 30 }
,,	←	−140	−175 dead to living
Coil at a distance ($\frac{1}{20}$).			
9	→	− 53 }	−1060 } living to dead
		+ 2 }	+ 40 }
,,	←	− 61	−1220 dead to living
18	→	−111	−2220 living to dead
,,	←	−142	−2840 dead to living

There can therefore be no doubt that in nerve also the + intrapolar after-current is a phenomenon connected with the aneletrotonic state.

The text shows that exceptions to this rule sometimes occur, as, for instance, when strong currents have been employed, in which case the + phase appears not only with currents directed from living to dead tissue, but also with those directed from dead to living; but this is not perplexing, for, as I have repeatedly stated in former communications, nerve cannot be stretched to such a degree as to get rid of the wavy form of its fibres, hence, with currents directed through its length, there must be multiple anodes and kathodes.

Biedermann[1] has recently drawn attention to the fact that, under exactly similar conditions, currents directed from dead to living tissue must in part enter the fibres in their length instead of their cross-section owing to unavoidable bends, etc. Muscle can be much more stretched without risk. In spite of this I hold the question as not finally decided whether or no anelectrotonus fails in the case of the strongest currents which are directed strictly from dead to living tissue; it involves principles of great importance and should be approached by special experiment.

[1] 'Sitzungsber. d. Wiener Acad.,' Part 3, vol. lxxxv. p. 144.

For the present sufficient material has been obtained to determine the correctness of my explanation of du Bois-Reymond's observations.

The phenomena of the extrapolar-currents, to the investigation of which we now turn, will render the decision of the point much more certain.

4. Investigation of extrapolar after-currents in Nerves and Muscles.

The extrapolar after-currents, following the passage of a current through a given portion of tissue, have been hitherto only investigated in the case of nerve. Fick was the first to observe that on either side of the polarising-current there appeared an after-current opposed to it in direction [1]. Shortly afterwards I entered on the same enquiry [2] and found that the two extrapolar regions were completely different in their behaviour; on the side of the anode I found, like Fick, an after-current opposed in direction to the previous current, on that of the kathode, however, an after-current, similar in direction to the previous current; the former was much more marked than the latter. On repeating his experiments Fick obtained results similar to mine [3]. Du Bois-Reymond mentions these phenomena, but does not state whether he has ever experimented upon the subject or not.

Since the publication of the work I did at that time, I have often had the opportunity of observing again the extrapolar after-currents of nerve, especially in the years 1871, 1872, when I was investigating the extrapolar after-currents in the case of platinum wires surrounded by fluid [4]. The new work of du Bois-Reymond and the explanation which, I believed, should be given to his supposed 'positive polarisation,' prompted me to a systematic re-investigation. As a matter of fact, the old experiments could not be considered as exhaustive, since in these the multiplier was used, the sluggish needle of which would not answer to a rather rapid change of current-direction; moreover, du Bois-Reymond's results encouraged making experiments with high strengths of current (which were

[1] 'Centralblatt f. d. med. Wissensch.' 1867, p. 436.

[2] 'Untersuchungen zur Physiologie der Muskeln und Nerven,' Part 3, p. 71. Berlin, 1868.

[3] 'Untersuchungen aus dem physiol. Labor. d. Züricher Hochschule,' Part 1, p. 129. Vienna, 1869.

[4] Pflüger's 'Archiv,' vol. v. p. 267; vol. vi. p. 318.

formerly viewed with distrust) and with very short durations of closure. Finally, the investigation had also to be extended to the case of muscle.

The method of experiment was that described previously in this communication, the leading-off electrodes being now extrapolar. The insulation of the two circuits by means of a paraffin commutator proved quite effectual also for these experiments, although, as I knew from previous work, the disturbing effect of bad insulation is more marked in the case of extrapolar than in that of intrapolar experiments. This latter circumstance is easily explained; for if the material of the commutator is at all conductive, then, during the closure of the battery circuit, derived currents will pass through the galvanometer which, in the case of extrapolar leading-off, must, however derived, be similarly directed through the instrument, whereas in the case of intrapolar leading-off these would be opposed in direction, and consequently would in part compensate each other; in this last case it is as though the galvanometer was introduced into the cross wire of a Wheatstone's bridge.

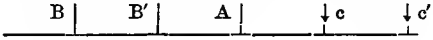
A large number of experiments, with currents of from 1 to 18 zinc carbon elements and of durations of closure from 1 to 60 seconds, establish the following propositions.

The deflection is in the case of nerve always in accordance with my previous observations; that is, on the side of the kathode it is +, similar in direction to the previous polarising current; on the side of the anode it is —, opposed in direction to the previous polarising current; in other words, it is, in both situations, directed away from the led-through portion of tissue. The anodal after-current is without exception stronger than the kathodal as I had previously found. But further, the light magnet of the galvanometer brought into view a new fact, viz.: the appearance, before the — anodal after-current, of a short + effect. *The anodal after-current is thus diphasic, i. e. first +, then —; the kathodal after-current is entirely +.* Moreover the — anodal after-current is of long duration, the magnet after reaching the maximum of its deflection returns slowly and incompletely, often remaining stationary, whereas the kathodal + deflection ceases immediately and completely.

In the case of muscle, (the sartorius stretched out on cork being generally used in these experiments) the law of the extrapolar after-currents, which are always very well marked, is in general the same as in that of nerve. A fact, as we shall see, of great import-

ance is the strength of the first + anodal after-current relatively to the second — effect, the former with weak currents frequently appearing alone; further the second phase is not, as in the case of nerve, stronger than the kathodal after-current, but on the contrary is always markedly weaker; it is, however, always of longer duration. The law for muscle may therefore be expressed as follows: *on breaking a polarising current, there appears on each side an after-current having the same direction as the previous polarising one (i. e. +); this is followed on the side of the anode by an opposed — deflection of long duration, whereas on the side of the kathode the + after-current shows no such opposite phase, but attains a very marked strength and then completely disappears.* In a few instances (of which the second example is one) I saw with weak currents, a double effect, first + then — on the side of the kathode. The following are examples of the facts described.

Example of an experiment on nerves. Two sciatic nerves placed side by side in alternating directions (as in previous experiments). Extrapolar leading off at CC′. Duration of closure short as possible.



Long polarised region AB.			Short polarised region AB′.		
Number of cells.	Direction of polarising current.	After-current in cc′.	Number of cells.	Direction of polarising current.	After-current in cc′.
1	←	+ 8 / −25* a	1	←	+ 8 / − 6 a
,,	→	+ 21 c	,,	→	+ 6 c
3	←	−117 *a	3	←	+ 5 / − 36* a
,,	→	+ 52 c	,,	→	+ 23 c
9	←	+ 20 / −154* a	9	←	+ 25 / − 91* a
,,	→	+ 75 c	,,	→	+ 50 c
18	←	+ 11 / −174* a	18	←	+ 20 / −108* a
,,	→	+ 54 c	,,	→	+ 39 c
,,	←	+ 25 / − 70* a			
,,	→	+ 32 c			

Another example on nerve. Arrangement as in preceding experiment, polarising current led through AB and AB′ alternately. Short duration of closure.

Number of cells.	Polarising current led in at	After-current in cc′. With direction of polarising current. ←	After-current in cc′. With direction of polarising current. →
1	A B	+ 5 / − 5 } a	+ 5 c
,,	A B′	+ 12 / − 6 } a	+ 14 c
3	A B	+ 10 / − 29* } a	+ 13 c
,,	A B′	+ 6 / − 61* } a	+ 27 c
9	A B	+ 12 / − 65* } a	+ 33 c
,,	A B′	− 114* a	+ 50 c
18	A B	+ 9 / − 70* } a	+ 48 c
,,	A B′	+ 9 / − 93* } a	+ 30 c

Examples of experiments on muscle. Sartorius, extrapolar leading-off contacts at cc′. Polarising current led in at AB; short duration of closure.

A | | B ↓c ↓c′

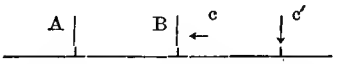
Example 1.			Example 2.		
Number of cells.	Direction of polarising current.	After-current in cc′.	Number of cells.	Direction of polarising current.	After-current in cc′.
1	←	+ 46 a	1	←	+ 35 a
,,	→	− 4 c	,,	→	+ 2 − 44 } c
,,	←	+ 20 a	,,	←	+ 30 a
,,	→	− 4 c	,,	→	+ 1 − 56 } c
3	←	+ 32 a	,,	←	+ 30 a
,,	→	0 c	,,	→	+ 1 − 28 } c
9	←	+ 3 − 15* } a	3	←	+ 55 a
,,	→	+ 156 c	,,	→	+ 17 c
,,	←	+ 15 − 32* } a	,,	←	+ 41 a
,,	→	+ 162 c	,,	→	+ 48 c
,,	←	+ 30 − 60* } a	9	←	+ 42 − 16* } a
,,	→	+ 153 c	,,	→	+ 394 c
18	←	+ 17 − 136* } a	,,	←	+ 64 − 47* } a
,,	→	+ 339 c	,,	→	+ 436 c
,,	←	+ 17 − 183* } a	,,	←	+ 35 − 15 } a
,,	→	+ 328 c	,,	→	+ 485 c
			,,	←	+ 58 − 12 } a
			,,	→	+ 402 c
			18	←	+ 30 − 255* } a
			,,	→	+ 542 c
			,,	←	+ 30 − 185* } a
			,,	→	+ 468 c

We postpone the explanation of the appearances observed to the next section. From experiments with intrapolar leading-off, it was to be expected that the phenomena would also appear more forcibly with extrapolar leading-off, if one leading-off electrode was united

with one of the polarising electrodes, and the extrapolar led-off part brought thus immediately up to the polarised region. One leading-off electrode was therefore placed with its kaolin point on the kaolin of one of the leading-in electrodes.

In this case the phenomena appeared still better and with more regularity than they did with the ordinary method.

Example of an experiment on nerve. Two sciatics lying side by side in alternating directions. Leading-in contacts at AB. Leading-off contacts at cc′. Electrodes c and B united. Short duration of closure.



Number of cells.	Direction of polarising current.	After-current in cc′.
1	←	+ 1 / − 31* } a
,,	→	+ 8 c
4	←	+ 3 / − 200* } a
,,	→	+ 111 c
9	←	+ 5 / − 247* } a
,,	→	+ 186 c
18	←	+ 90 / − 227* } a
,,	→	+ 296 c

Example of an experiment on muscle. Sartorius, led in and off as in the preceding case of nerve.

Number of cells.	Direction of polarising current.	After-current in cc.
1	←	+ 60 / −127* } a
,,	→	+ 56 c
4	←	+ 20 / − ∞* } a
,,	→	+123 c
		Bobbin removed to further distance from galvanometer ($\frac{1}{18}$). reduced values.
,,	←	+ 2 / − 38* } a = + 36 / −684*
,,	→	+ 5 c = + 90
9	←	− 53* a = −954*
,,	→	+ 11 c = +198
18	←	+ 14 / − 43* } a = +252 / −784*
,,	→	+ 12 c = +216

Finally, it may be stated that I have made a number of experiments with Herr von Gendre's help, upon nerve and muscle led-off intrapolarly and extrapolarly at the same time, in order to determine the time relations of the two phases. But as these experiments offer no new point of view, I omit further reference to them.

5. Explanation of the intrapolar and extrapolar after-currents of Nerves and Muscles, together with further experiments.

A. The after-currents which arise from true polarisation.

Since its discovery by Peltier, it has been accepted by all observers that the opposed — after-current, which appears in the intrapolar region of a length of nerve or muscle, through which a current has been led and broken, is due to internal galvanic polarisation. This current shows, in fact, unmistakeably all the peculiarities of a polarisation current. Especially noticeable is its rapid decline, as evidenced by the fact, that only slight traces of it can be found when a short time is allowed to elapse between the breaking of the battery and the closure of the galvanometer circuit. The

aperiodic magnet shows this characteristic most plainly by its mode of movement, which does not at all follow the laws which hold for persisting currents [1], the first part of the deflection being very rapid as compared with the later part, and in the case of light magnets often only a momentary jerk; evidently the current has perceptibly decreased before the deflection has had time to occur; hence the deflection is smaller with strongly damped than with slightly damped magnets, apart from the delicacy of the galvanometer. (Compare the above-mentioned experiments with two galvanometers.) Moreover, the relation of the opposed — after-current with the strength and duration of the polarising current is quite of the same kind as in ordinary polarisation [2].

As is well known, du Bois-Reymond was the first to indicate that the seat of this 'internal' polarisation is by no means entirely confined to the electrodes of the polarising current, but is spread over the whole led-through region [3]. Since many porous materials, when moistened with electrolytic substances, show an internal polarisation, which may be explained as due to the formation of ions, du Bois-Reymond applied this explanation to the internal polarisation found in led-through muscle and nerve, these tissues being both porous and electrolytic (du Bois-Reymond, Sect. 3).

By experiments with my conducting axis schema, I have demonstrated and explained the phenomenon of internal polarisation, and I have further shown that known physical conditions are effectual for its production in the case both of nerve and of muscle. This former explanation of mine receives now additional support from the fact that it can also be applied to the extrapolar after-currents of nerve and muscle. For brevity I denote by conducting axis schema, a wire enveloped by an electrolytic material, into the envelope of which a current is led, it being indifferent whether the envelope is the twisted thread soaked in fluid used by Matteucci, or the fluid contained in a small tube used by myself. A wire thus enveloped in fluid shows, just as muscle and nerve show, opposed polarisation after-currents throughout its intrapolar region [4]. (An exception presents itself when the connection is unpolarisable, such as an amalgamated zinc wire in solution of a zinc salt.)

[1] See du Bois-Reymond on aperiodic magnets.
[2] See Tigerstedt's paper on internal polarisation, p. 80 of this volume.
[3] 'Untersuchungen über thierische Elektricität,' i. p. 377; ii. 2, p. 378.
[4] See Pflüger, 'Archiv,' vi. p. 319.

Before passing on to the extrapolar phenomena shown by the conducting axis schema, it is first necessary to supplement in some points the theory and experiments previously set forth.

The polarisation after-currents in the conducting axis schema (Kernleitermodell).

(a). Experimental.

Several circumstances made it desirable that the experiments, carried out in 1871-72, upon the after-currents of the conducting axis schema, should be repeated and supplemented. First, that these had been made only with moderate strengths and long closures of current; consequently, having regard to du Bois-Reymond's experiments, the effects of strong currents and short closures had still to be investigated. In the second place, in my former experiments I broke the polarising current and then closed the galvanometer circuit by a key; it was therefore desirable to arrange for a more rapid succession than this gave, so that the conditions immediately following the break might be determined. Finally, it remained to be seen whether the use of the galvanometer with light magnet, which I now employ, would bring into view new phenomena, such, for instance, as change of direction of after-currents.

For most of my experiments I used tubes filled with solution of sulphate of zinc, and provided with side openings; the tubes were 4½ mm. in internal diameter, and from 40 to 196 cm. in length[1]. Through the tubes were drawn platinum wires either very fine or of ordinary thickness. The four electrodes were amalgamated zinc wires with bayonet-shaped bent ends, thrust into the side tubes; the bayonet-shaped bends gave such support that the wires only reached as far as the upper surface of the main tube. The alternate closure of battery and galvanometer circuits was effected by means of the previously described paraffin commutator. The battery was 1–18 zinc carbon elements. The delicacy of the galvanometer was diminished to the requisite degree by distancing its coils.

I have previously stated that, with a combination polarisable in two ways, the extrapolar after-current is opposed in direction to

[1] In the latter case they were made up of several shorter pieces of tube joined by elastic tubing. Some of my tubes have many side openings close to one another, others have a few some distance apart. Long tubes were generally so made up that the side openings were near one another at the two ends, far apart in the middle.

the polarising current, and that it is connected with the actual production of two oppositely polarised axial regions; that, on the other hand, with one-sided polarisation the extrapolar after-current is in the same direction as the polarising current. The first condition is present when a platinum wire is immersed in sulphate of zinc solution or weak sulphuric acid, and the polarising current is led in at two points in the fluid; the second occurs when a copper wire is immersed in weak sulphuric acid, and the current is led in at two points in the fluid, also when a platinum wire is similarly immersed, and one leading-in electrode is connected directly with the wire [1].

These two main facts were supported by the new experiments. In addition, however, the following facts were ascertained:—

(1) With platinum wire in zinc sulphate solution light magnets show an extrapolar after-current which is exclusively — on both sides, provided the polarising current is of moderate strength; when stronger currents are used, this — current is preceded, on the anodal side, by a rapid + effect, in consequence of which the prevailing — after-current appears to be much weaker here than on the kathodal side, where no such previous effect appears. When very strong currents are used the + effect on the anodal side may quite overpower the — one.

(2) With platinum wire in weak sulphuric acid the extrapolar after-current generally remains — even with the strongest currents. The arrangements for this experiment in which a fluid, other than zinc sulphate, is employed, have been most advantageously modified so as to do away with the tubes bound round with membrane (see Pflüger, 'Archiv,' vi. p. 319). The side openings of the experiment tube having been filled to the brim with zinc sulphate solution, were closed by elastic tubing caps into which glass plugs were fitted; into the four side openings used for leading in and off, amalgamated zinc wires instead of glass plugs were introduced and fixed. The main tube was now turned through 180° so that the side tubes pointed downwards, and the zinc solution was poured out of the tube, the side tubes alone remaining full; the fluid to be experimented with was now injected or aspirated into the tube: it was thus brought above the zinc without disturbance of any kind.

(3) With a very thin envelope of fluid surrounding the platinum

[1] See the method of experiment as described in Pflüger, 'Archiv,' vol. vi. p. 312, 319.

wire the extrapolar currents are + on both sides of the polarising current. For experiments of this kind I used Matteucci's arrangement, i.e. platinum wires surrounded with twisted cotton soaked in sulphate of zinc; leading in and off was effected by means of amalgamated zinc wires bent into hooks and applied to the stretched wire. I have also used two cables made up of many fine platinum wires which behave exactly like the single covered wire. A very long, fine platinum wire, thickly covered with fine silk, was cut into a number of equal lengths, and these bound together so as to make a cable, which was then itself covered with silk; one such cable contained 30, the other 100 wires (those of the first were 28, of the second 57 cm. long). Both cables, after soaking well in sulphate of zinc, gave on each side of the polarising current + extrapolar after-currents. The same results were obtained after soaking the single wire, or the cable, in other fluids. Kaolin electrodes were used for leading in and off.

(4) The difference, stated above, in the behaviour of thin and thick fluid envelopes, and the theoretical considerations connected with this difference, made it desirable to observe the changes in the behaviour of the extrapolar after-currents with varying thicknesses of fluid envelope.

I have not as yet been able to accomplish this in the case of the tubes and wires. The end seemed more attainable in those cases in which the conducting combination had a wide-spread surface. To obtain this, I covered the floor of a Bunsen's mercurial bath with mercury, and poured upon this a thin film of sulphate of zinc. For leading off and in the zinc wires dipping into the fluid were not used, as these were liable to disturb the mercury, but tube electrodes were employed, the kaolin points of which, saturated with zinc sulphate, rested upon the fluid.

With axially arranged leading in and off contacts, the entire extrapolar surface of the fluid showed an after-effect similarly directed to the polarising current +. As the film of fluid was gradually increased in thickness, the after-effect in the neighbourhood of the electrodes became − or + −, at a distance from the electrodes it remained +, by further increase in thickness, the after-effect everywhere became + −, or − only. There is, therefore, a certain thickness of fluid with which the extrapolar after-current shows at a certain distance from the electrodes a 'turning-point,' or 'line,' inside which it is −, outside +. The thickness in question is dependent upon the strength of the polarising current; reversal

of current gives predominantly double, + −, effects. The observations are very variable, owing to inequalities in the surface of the mercury, so that I have not followed out these experiments further. They sufficiently establish the above-mentioned 'turning point.'

(b). Theoretical.

I have previously shown that a current led through a portion of the schema spreads, on account of resistances round the core, very widely into the extrapolar regions, so much so that + currents are indicated in galvanometer circuits connected with the schema at considerable distances from the led-through part; these correspond to the electrotonic currents of nerve and muscle. At the same time polarisation occurs through the formation of ions round the core, the distribution of which may be expressed by a double curve. This curve has its positive maximum at the anode of the polarising current, the negative maximum at the kathode; it cuts the abscissa at a point in the intrapolar region (the indifference point), and approaches the abscissa in the extrapolar regions asymptotically.

This distribution of polarisation is the key by means of which the physiological effects described as electrotonic appearances become intelligible.

On breaking the polarising current this polarisation equalises itself by inner currents, which are indeed present during the passage of the led-through currents and can weaken or strengthen the latter according to their direction.

If we take an extrapolar region by itself without reference to the rest of the conducting schema, then this must, as is easily seen, show a + after-current (i.e. in the same direction as the polarising current). On the side of the anode, for instance, the core is, in the extrapolar region, polarised positively (the platinum wire, if in zinc sulphate, being covered with zinc), in less and less degree the further from the anode, consequently every point nearer the anode is positive to one further off. A leading-off circuit connected with this region will therefore lead off a current directed through it, from the anodal to the further point of connection; in the same direction, that is to say, as the polarising current has in this circuit. Similarly, on the side of the kathode, every point nearer the kathode is negative to one further off (in the schema becoming covered with SO_4, i.e. sulphuric acid and oxygen), so that here again a circuit must lead off a + current.

This relation is present in all cases where there is no disturbance from the formation of oppositely polarised regions; above all, in cases in which the current is led through the schema with one leading-in electrode attached directly to the core. On each side of the remaining single electrode the core is similarly polarised, and this in regularly decreasing degree, so that on each side of the electrode a current is found which, without exception, is directed either from or to it, according as it is an anode or a kathode (taking the direction of the current in the leading-off circuit). I have convinced myself by special experiments that it is indifferent with which end of the core the other pole of the polarising current is joined. It is easily conceived that in this simplest 'unipolar' case the distinction between intra- and extra-polar leading-off, and the description of after-currents as + and − are inadmissible, since both expressions change when the polarising circuit is directly joined first to one then to the other end of the core, without any variations being manifested in the after-currents.

A second case in which the extrapolar relations appear undisturbed as above, is that in which the combination is only capable of polarisation on one side, and the extrapolar leading-off is on the side of the polarisable electrode.

A third case will be mentioned later on.

These extrapolar conditions, causing currents which, for short, I may be allowed to describe as 'idiopolar,' will be disturbed by the presence in the core of another oppositely polarised region. The two regions seek to equalise their polarisations by currents which run through the fluid from the anodal to the kathodal parts, and which are thus when led-off − in character (i.e. directed through the leading-off circuit in opposite manner to the polarising-current); these I propose to describe as 'bipolar' currents. Eleven years ago I proved experimentally that these opposed currents were connected with the presence of two oppositely-polarised regions of the core.

In the intrapolar region, the bipolar current evidently must always be directed similarly to the idiopolar currents which would be shown on either side of the indifference-point in each half of the region. In the intrapolar region, therefore, the after-currents under all circumstances, as well in combinations, polarisable on one side only as in these, must be −, and this is borne out by all experiments.

Much more complicated are the conditions of the extrapolar regions with doubly polarisable combinations. Here the bipolar-current is opposed to the idiopolar, and the ultimate condition must

therefore, depend upon the extent to which the former can spread into these regions. It is evident that this state of affairs must be at a minimum for the distance in which the extrapolar polarisation is at its maximum. The maximal polarised regions in themselves will have no idiopolar-currents, but only currents between one another, which, if led off, would be — in character, just as two pieces of metal in fluid give a considerable bipolar-current. Mere observation readily shows that when the fluid cylinder is large, the deposition of zinc on the one side, and the development of gas on the other, spreads, even with moderate strength of current, far out into the extrapolar regions, whereas, on the other hand, in the intrapolar region both are invisible quite close to the electrodes, provided that this region be not very long. There can be no doubt that where the ions are visible the maximum of polarisation has been reached, and that this maximum may stretch still further out. But on account of the good conduction of the core, the bipolar-current must spread in the fluid beyond the region of maximal polarisation, the effect of which is that the surfaces of potential proceeding from the maximal polarised portions, independent of the decreasing tension due to the proper polarisation of the parts superficial to the core, run almost concentrically along the core, and in consequence the *idiopolar*-current of the extrapolar region must be almost or quite concealed. As a matter of fact I have never succeeded, after numberless experiments with tubes $1\frac{1}{2}$ metre long, and with the finest wire core, in ascertaining a 'turning-point' in the extrapolar region, although such a point certainly must theoretically exist. The bipolar-current, when it is present, spreads so far into the extrapolar region that on reaching a position where the idiopolar current alone might occur, the polarisation effects have dwindled almost to nothing. (See Pflüger, 'Archiv,' vol. vii. p. 317.)

It is quite otherwise in the case of very thin envelopes of fluid. In the first place, the fall of polarisation effect is here much steeper, since the intensity of the lines of current entering the core must decrease much more rapidly in proportion to their distance from the led-through region, this more rapid decrease being due to the much more marked inequalities in their length. In the second place, a greater resistance is offered to the passage of the bipolar currents, and moreover, the conditions are not favourable for their extrapolar spread. In this case, too, the distribution of tension upon the surface of the thin fluid envelope must be a true expression of the distribution upon the core itself. So then here the idiopolar

must come into operation with but slight disturbance, and the 'turning-point' must nearly coincide with the electrode itself. It is thus that wires with thin fluid envelopes give + extrapolar — intrapolar after-currents.

It might thus be predicted that if the thickness of the fluid envelope could be increased by successive steps, then, with a 'two-sided' polarisable combination, a 'turning-point' would be found in the extrapolar region, which would rapidly move to a greater distance from the electrode in proportion as the envelope increased in size. This prediction is fufilled by the results of the above-mentioned experiments with the mercury trough.

Considering the unavoidable conflict in all cases of 'two-sided' polarisation between the idio- and bi-polar currents, it is not surprising that after-currents are found directed both ways, although it may be difficult to explain the phenomena with exactitude. An extrapolar after-current, first + and then —, such as occurs with currents of medium strength at the anode of a platinum zinc sulphate schema, would thus mean that in the first moment after the polarising-current was broken the idiopolar current had the mastery, but that in a short time it gave way before the bipolar current; whilst with stronger currents only the latter can be observed[1]. With certain exceptions the decrease in the extrapolar tensions obviously offers a ground for this expression of the state of affairs; but its actual truth might be shown by special experiments, for which however there is no urgent present necessity, since, as we have seen, this special condition does not occur in the case of nerve and muscle. The fact that the biphasic extrapolar after-current of the platinum zinc sulphate schema is more easily produced on the side of the anode than on that of the kathode is possibly connected with the covering of the wire on the kathodal side by a badly-conducting gaseous layer. In favour of this view is the fact mentioned previously that with a platinum in sulphuric acid schema, in which there is development of gas at both poles, the phenomenon appears but seldom and then only in a very rudimentary manner.

Here, then, I conclude the investigation of the polarisation after-currents of the schema. To give a complete theoretical representation of the tension and current distribution would be im-

[1] This may be expressed also as a moving of the 'turning-point' further out. The connection of this phenomenon with one long observed by me in such schemata will be brought forward in another treatise.

practicable, as everyone versed in the mathematical laws of the subject will admit, since for its expression it would be first of all necessary to state the distribution of polarisation upon the surface of the core at the moment of break. This distribution, however, changes with the very currents which tend to equalise matters, and these currents themselves vary under the influence of the resistance of the gaseous ions. The principal points are, I believe, sufficiently explained by the foregoing experiments and theoretical considerations, I therefore refrain from giving the approximate distribution charts which I have prepared of the chief cases.

Let us now go back to muscle and nerve and see what polarisation after-currents are to be expected in these tissues.

The polarisable combination of core and envelope in muscle and nerve is, as I have previously shown[1], a 'doubly polarisable' one. We infer this—

(1) From the approximately equal size of the electrotonic current branches in the anodal and kathodal regions.

(2) From the existence of two separate oppositely polarised regions, with intermediate indifference-point, as testified to by the well-known excitation phenomena of an- and catelectrotonus.

The envelope may be regarded as very thin, the conductivity of the core as in no way relatively great. Without doubt, therefore, with these tissues the state of matters is this, that the polarisation bipolar after-current does not spread into the extrapolar regions. So that these only show the idiopolar after-current as in the case of the platinum wire schema with thin fluid envelope.

The polarisation after-current in muscle and nerve must therefore be — (opposed to polarising-current) in the intrapolar, + in the extrapolar region.

B. The after-currents proceeding from the break-excitation.

A number of facts have established that it is the anelectrotonic region which is excited both in muscle and nerve at the moment of break, and that this region may remain in prolonged excitation on the break of a very strong current or one of long duration. Notably, Pflüger has shown, by a beautiful experiment, the connection of Ritter's breaking tetanus in nerve with the excitation produced by a disappearing anelectrotonic state; in muscle, indeed,

[1] See Pflüger, 'Archiv,' vols. v., vi., vii.

the prolonged breaking excitation reveals itself at the anode by the bulging of the tissue[1].

There is no doubt that this excitation is strongest at the anode and decreases in intensity in proportion as the distance from the anode increases. According, therefore, to the law of currents of action, nerve and muscle, after the break of a sufficiently strong current, must be the seat of currents of action which are directed in the tissue away from the anode on both sides.

For completeness it may be further stated that another current of action may be present after the break of a current of very short duration, namely, the action-current produced at the kathode by the make of the polarising-current. This will undoubtedly be present during the early part of the time of closure, and there is no decided reason why it should not continue longer than the polarising current if the time of closure of the latter is very short; it certainly would not be of marked character, since, in the first place, the polarisation opposed current is unfavourable to the persistence of the kathodal excitation (the kathode now becoming the anode); and, in the second place, I have never been able to see after short closures any bulging of muscle at the kathode, which would remain synchronous with a bulging at the anode.

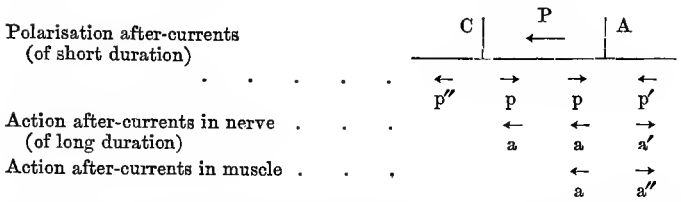
This kathodal action-current would evidently be opposed to the polarising current when intrapolar, + when extrapolar; it has, therefore, in all cases the same direction as the polarisation after-current, so that it could be differentiated from the latter at most by its longer duration. As however such long duration is not observable we may omit this current, and therefore it will be disregarded in what follows. It will be referred to once again later on.

C. Combination of the polarisation and excitation after-currents. Explanation of the secondary electromotive phenomena.

The anodal current of action is similarly directed to the polarising-current (i.e. +) in the intrapolar, oppositely directed (i.e. —) in the extrapolar region, it completely fails in the kathodal extrapolar region. Whenever it appears, it is, therefore, opposed to the polarisation after-currents and comes into conflict with these.

The whole relation is seen at a glance by means of the following schema, in which the arrow P indicates the polarising current, A and Ç the anode and kathode.

[1] See 'Handbuch,' Hermann, vol. i. p. 93.



It lies in the nature of the excitation after-current that it should be much more prolonged than the polarisation after-current, which as well in the tissues as in the conducting axis schema, in all cases rapidly disappears. Nothing is more natural therefore than that the conflict of the two currents should express itself in the double character of the after-currents actually observed, the first phase of which always indicates the polarisation, the second the action-current. Further, the more the action-current is developed in comparison with the polarisation-current, the more will the first phase of the doubly-directed current tend to disappear, as also must be the case when the magnet has a slow swing.

We have therefore to expect that—

(1) The intrapolar region should show an after-current which is first — (opposed to the polarising-current), and then + :

(2) The anodal extrapolar region an after-current first + and then — :

(3) The kathodal extrapolar region an after-current which is always +.

Now the relations established by experiment agree in all points with these. That given above under 1 is the actual condition as stated in du Bois-Reymond's treatise, those given under 2 and 3 were stated previously by myself and A. Fick, and are fully established by the present investigations.

It is further readily intelligible that the intrapolar action-current, du Bois-Reymond's second positive phase, should only appear after currents which are strong and of short duration; strong, because only then is the breaking excitation sufficiently prolonged to overlap the polarisation after-current, and of short duration, because the latter current is not so markedly developed by short as it is by long closure, and thus the complete concealment of the action-current by the polarisation is not so easily produced.

Further proof of the correctness of my explanation is furnished by the circumstance discovered by du Bois-Reymond himself, that his positive phase, our current of action, is intimately connected

with the vitality of the tissue, whilst the first negative phase, our polarisation-current, occurs in dead tissues so long as their structure is not destroyed. The unproductive speculations of du Bois-Reymond connected with these relations are thus very simply settled.

Finally, the most convincing proof lies in the fact, quite overlooked by du Bois-Reymond, and now established by myself, that the intrapolar + phase of muscle is connected in the most pronounced manner with neighbourhood to the anode, whilst there is no trace of the − phase there. It is obvious that the indifference-point, even with the strongest currents, does not move so far towards the kathode in muscle as in nerve; so also the spreading of polarisation and the electrotonic currents do not extend so far in muscle as in nerve.

It is therefore not to be wondered at, as has been already remarked, that the + phase in nerve should appear equally well in all parts of the intrapolar region, since with currents of the strength used in these experiments the indifference-point is brought, as Pflüger has shown, quite close up to the kathode[1].

This is the place to mention a set of experiments which I have conducted on consideration of the fact that Ritter's tetanus is produced even by currents of moderate strength when these are kept closed for some time, half an hour for instance. In such a way I hoped to be able to bring out the + intrapolar phase with weak currents (one zinc carbon cell). The nerve was left attached to the leg so that the breaking tetanus might be present as a control. But after half-an-hour's closure a very strong and abnormally long − deflection was all that appeared during the violent breaking tetanus; that is to say, the long closure had developed polarisation of a much more marked and more slowly vanishing character than would otherwise have been the case, so that this fully compensated the current of action. This experiment however shows the interesting result that *Ritter's tetanus is connected with a polarisation of the nerve which remains for a long time after the break.*

The above statements also disfavour the theory of the breaking excitation recently set forth by Tigerstedt and Grützner[2], which, after reading Grützner's detailed work[3], I hold to be erroneous. We see after the short closure of a strong current, the intrapolar current of action immediately appearing; that is to say, the

[1] See previous remarks upon electrotonic spread.
[2] See my previous remarks in Pflüger, 'Archiv,' vol. xxxi. p. 99.
[3] Pflüger, 'Archiv,' vol. xxxii. p. 357.

breaking excitation here lasts much longer than the polarisation after-current. The breaking excitation cannot therefore be directly dependent at any rate upon the establishment of this polarisation-current.

To this it may be objected that the long prevalence of an action-current does not prove that a polarisation-current is not present, it may be there all the time but overpowered. On the kathodal side, however, we see how quickly, *in all cases*, the polarisation-current vanishes. Further, so long as the action-current lasts, even though a portion of the polarising-current be present, so long is the anodal region practically one where current enters, not leaves, as the above theory requires. The break-excitation is therefore dependent upon changes which the current has left in the tissue upon the disappearance of positive polarisation, whether this disappearance occur by a polarisation opposed current or by any other process of removal of electrolytic products. A number of objections to Grützner's last publication may be reserved for a later opportunity [1].

The extrapolar phenomena of muscle and nerve can be as completely explained as the intrapolar. The facts discovered by me some time ago with the multiplier, namely + after-current in the kathodal, stronger — after-current in the anodal extrapolar region of nerve, are now recognised as polarisation and action-currents respectively [2]. By using a lighter and more aperiodic magnet we

[1] A few points only I must mention here. First, with regard to the experiments made by me in 1875 upon the connection of the polarisation opposed current with the breaking contraction, and now first communicated. These experiments, as I can show most accurately from the records, were made with leading-in contacts at a great distance from the cross-section. Happily the positions of the electrodes were marked and fixed on the myograph papers which have the muscle tracings. In the second place, the conclusion which I draw from these experiments is not of recent date, but was arrived at eight years ago, the whole experiment being, indeed, conducted with this in view. I am able, by documents, to prove this to any who may be interested in the matter. Its present publication is due to the fact that an investigation into the nature of nerve-excitation, reaching back to the year 1871, and for which I have collected a mass of experimental material, has only recently appeared to me sufficiently advanced to permit of its publication; some part has already appeared in this 'Archiv.' In the third place, Grützner has cited a discrepancy of Tigerstedt's as in disagreement with my law of the polarisation increment. I have already shown in another place the insufficiency of the discrepancy—a fact which Grützner cannot have known (Hofmann and Schwalbe's 'Jahresbericht,' 1882, ii. p. 19.)

[2] Following out a suggestion made by Pflüger, I assigned this latter explanation, eleven years ago, to the phenomena of the catelectrotonic region, as I then erroneously believed that the extrapolar polarisation currents in nerve must be — in character, being led to this by my experiments with the schema having an envelope of thick fluid (see Pflüger, 'Archiv,' vol. vi. p. 357).

have learnt that the former rapidly disappears, the latter remains for some time persistent; and, further, that the latter is preceded by a rapid + condition, which is the polarisation-current of the anodal extrapolar region. Moreover, we have established the same laws for the phenomena in muscle also. There is here only a quantitative difference. In nerve the anodal − action-currrent is so strong that, although it has to contend with a + polarisation-current, it is still able to exceed in magnitude the undiminished + polarisation-current of the kathodal region. In muscle this is not the case; the action-current is indeed strong, but when weakened by the polarisation-current, it sinks below the magnitude of the full polarisation-current of the other region. In the schema (given under C) this may be indicated by stating that in nerve $a' - p' > p''$, or if $p' = p''$, then $a' > 2\,p'$; whilst in muscle, $a' - p' < p''$, or $a' < 2\,p'$. The weak development of the extrapolar breaking-excitation in muscle may be due either to a weak development or to a rapid disappearance of the anelectrotonic state. It is noteworthy that we find the intrapolar spread of anelectrotonus to be less in muscle than in nerve.

In his second publication, on the extrapolar after-currents of nerve, Fick suggests that the kathodal after-current, which he had stated in his first communication to be −, like the anodal, might possibly be − in the first moment after opening, and then +, thus being double in character. This suggestion now appears to be a faulty one. As a matter of fact it is the anodal and not the kathodal-current which is double in character, being first + and then −. We are able now to substitute for the view, which led Fick to this suggestion, something more certain, viz. the complete explanation of the causal relations.

Finally, we obtain some explanation of a long-known phenomenon. Pflüger by excitatory[1], and du Bois-Reymond[2] by galvanometric methods, found that during the closure of a polarising-current the extrapolar anelectrotonic state tends to increase, the catelectrotonic state to decrease. This may be now fully explained as follows. The extrapolar polarisation (as in the metal and fluid envelope schema, vide Pflüger, 'Archiv,' vol. vi. p. 320) must strengthen the extrapolar currents on both sides the longer it continues. On the side of the kathode, however, we have at the commencement of closure an action-current of similar direction

[1] 'Untersuchungen über die Physiologie des Electrotonus,' p. 319.
[2] 'Archiv' f. Anat. u. Physiol. 1867, p. 441.

to the polarising current (see previous remarks) which tends rapidly to decrease. In consequence of this the kathodal current must first become stronger and then tend to decrease. The phenomena, during closure of the polarising-current, are therefore no less in accordance with the principles laid down than are those following its break.

6. Concluding Remarks.

The foregoing investigation has accomplished the task of explaining the phenomena of intrapolar after-currents as given by du Bois-Reymond; it has also introduced new facts; and further, it has widened our knowledge of the extrapolar after-currents, has extended these to muscle, and fully explained them.

There remain unnoticed, (with the omission of facts connected with electrical organs, in regard to which I could make no investigation, and of the after-currents which, at any rate, allow of explanation by means of our principles), certain statements of du Bois-Reymond as to the way in which 'positive polarisation' is favoured by the use of currents, the direction of which coincides with the natural direction of the excitatory wave; upon these phenomena the author lays very great weight (for muscle, see du Bois-Reymond, Sect. 10; for nerve, Sect. 17).

In respect to nerve, du Bois-Reymond's own statements are dubious, but in respect to muscle they are pretty decisive, although, strangely enough, the most conclusive method of experiment has not been employed, viz. that of leading through the entire muscle and leading-off the after-currents from two intrapolar regions in the two muscle-halves at the same time. But, before acquiescing in the far-reaching conclusions which du Bois-Reymond draws from these phenomena, it might be well to inquire what share the above enunciated simple laws, which have entirely escaped du Bois-Reymond's notice, may have in the production of the phenomena. I prefer, however, to leave this inquiry to du Bois-Reymond himself, merely hinting here at conditions which would suffice at once to explain the whole of this wonderful thing.

Du Bois-Reymond had, at the extremities of both muscles, fibres of which the ends were for the most part injured, as his intimations with regard to the currents of rest show. This circumstance which

has so often proved a source of danger[1], must, in accordance with the above-disclosed law, more or less impair the development of the + after-current, in the case of abterminal (from dead to living) direction of current, so that it would appear to be favoured in the case of atterminal direction of current, i.e. a direction like that of the excitation wave.

There is, therefore, no subject in the whole range of electro-physiology in which the connection of the phenomena is more transparent than that of the 'secondary electromotive phenomena,' which now extend to the extrapolar region. Du Bois-Reymond's 'curiosity' as to what 'auxiliary hypothesis' I shall advance to dispose of his positive polarisation-currents, will now be fully satisfied. The question, how far it is true that 'all that I have discovered concerning electrotonus' has 'been exploded,' that 'the elucidation of electrotonus must be approached anew,' and, finally, that I have been 'compelled' to 'import some changes into my scheme,' as to this everyone can now judge for himself. Happily none of these suggestions are true. The confusion which the molecular theory caused, in that it overlooked, whilst expatiating, what was most obvious, is luckily done away with now in this department of the subject, as it has long been in other departments, and everything has so turned out as to furnish fresh support to my explanation of the nature of the phenomena of animal electricity. When du Bois-Reymond deplores that he did not, in 1867, disclose to me the fact 'that there is positive polarisation in the intrapolar region,' because then 'the course of science in this direction would have been different, and perhaps more fruitful,' I can only agree with him, for then, possibly, we should have come to an understanding years ago as to this 'positive polarisation,' and du Bois-Reymond would have allowed the molecular theory, of which this is the last prop, to fall.

The molecular theory owes its production to the error of fact that uninjured muscles show as strong a muscle-current at their natural cross-section, as injured muscles do at their artificial cross-sections. When this was found to be an error, the theory was not given up, but the mischievous compromise of 'parelectronomy' was invented. Then, when I found the total absence of current in uninjured tissues, and parelectronomy no longer sufficed, (the 'cold hypothesis' brought to its aid being false as to its facts,) still the

[1] See for instance Pflüger, 'Archiv,' vol. xvi. p. 243.

theory was not abandoned, but every inconvenient case of absence of current was, on various pretexts, explained away. The molecular theory next introduced untold confusion into the subject of action-currents, where it literally turned things upside down ; errors of fact had to be first removed, and then new facts discovered before this confusion could be got rid of, and before this department of the subject could be so cleared up that its law, like that of the current of rest, could be expressed simply.

The molecular theory was especially unhappy in its application to electrotonus. It was incapable of explaining either the galvanic or the excitatory phenomena, although it pretended to explain the former and held out the prospect of explaining the latter, together with the function both of nerve and of muscle in its entirety, in the future. Now it has come to this, that on the one hand the theory claims to have discovered a fact basis for the supposed intrapolar arrangement of molecules (of course, only by disregarding obvious explanations), while on the other it abandons its explanation of extrapolar currents, notwithstanding that this intrapolar rotation was invented (it need scarcely be said without any basis of fact, or discussible theory) for the very purpose of explaining the extrapolar currents.

The theory was equally unfortunate in its application to the currents of the skin and secreting organs ; here it has favoured the setting up of an almost inverted law of secretion-currents, founded on a false conception of action-currents in nerve and muscle, and so has led to results which are wrong in fact. Finally, it has shown itself an utterly incapable guide in the study of electrical fish, the best that it could do being to bring into existence an easily demolished fabric of rash speculations. I will not refer to the currents of plants and parenchyma which, as they are in the highest degree inconvenient to the molecular theory, are wilfully neglected, or of which the facts are misrepresented.

I challenge the mention of a single statement contained in this indictment against the molecular theory which I am not able to substantiate and confirm by quotations. I maintain, however, that this theory which was sufficiently dangerous to lead its author (the creator of this rich field, the discoverer of its methods, the man who has helped to teach his contemporaries in medicine to think in accordance with physics) from error to error, that this theory must now at length be given up. It must be given up completely ; all toying with it in handbooks must cease, even at the cost of losing a

couple of pages of elegant schematizing. Nothing is so elegant as the simple truth.

But is there a single subject in physiology to which more simple and beautiful explanations are applicable, even to the finest details, than that of electro-physiology?

Four short, and more or less interdependent, propositions suffice to explain all the galvanic phenomena, with the exception of the shock of electrical fish and the 'action-currents' of the retina, neither of which are contradictory to them, although they may not as yet, admit of explanation by them. These propositions are:—

1. Localised death in continuity of protoplasm, whether caused by injury or by metamorphosis (mucous, horny), renders the dead part negative electrically to the unaltered part.

2. Localised excitation in continuity of protoplasm renders the excited part negative electrically to the unaltered part.

3. Localised warming in continuity of protoplasm renders the warm part positive, localised cooling the cold part negative to the unaltered part.

4. Protoplasm is strongly polarisable on its limiting surfaces (first shown as regards the protoplasm enclosed in tubes of muscles and nerves); the polarisation constant decreases on excitation (and on dying).

Besides, having disposed of the secondary-electromotive phenomena, the above investigation has furnished some not unimportant contributions to the physiology of muscle and nerve. Pflüger's statements as to the movement of the indifference-point have been verified for strong currents in a new manner, as well as the results of Biedermann, of Engelmann, and of Van Loon as to the effect of demarcation-currents upon the efficiency of 'physiological electrodes.' The electrotonus of muscle intra- and extrapolar has been established anew, and its complete analogy with the phenomena in nerve has been shown, together with the quantitative differences as regards its spread from the electrodes, especially from the anode. The time relations of the electrotonic spread in nerve have been as satisfactorily explained as the electrotonic after-currents. The intimate connection of breaking tetanus with long persistent polarisation has been proved, and a new position in the investigation of the nature of the breaking tetanus has been gained.

In relation to many further questions new methods of experiment have suggested themselves which will be better discussed when these experiments are published.

X

ON

THE PHENOMENA OF INHIBITION

PRODUCED BY THE

ELECTRICAL EXCITATION OF STRIATED MUSCLES, AND ON POSITIVE KATHODIC POLARISATION.

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Extraordinary Professor of Physiology in the German University, Prague.

Sitzungsberichte der kais. Akad. der Wissensch., Vienna. Part III. p. 142 (1885).

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1. Introduction.

[1] In the investigation of the secondary electro-motive phenomena in the adductor muscle of Anodonta [2], the most striking fact seemed, that here, quite contrary to the usual behaviour of the striated trunk muscles of the frog, not only positive anodic but also positive kathodic polarisation is observed, for on leading off from the anodic as well as from the kathodic half of the muscle traversed by the current longitudinally, occasionally an after-current of the same direction and frequently of very considerable strength appears, without simultaneous internal polarisation of the intrapolar tract of any importance at all. Hence, the inference is, that the cause of this phenomenon is to be sought solely in alterations of the substance of the muscle produced by the polarising current at its points of exit.

The anodic persistent excitation which follows on opening a current of corresponding intensity and duration of closing, explains positive anodic polarisation in a thoroughly satisfactory manner, as has been convincingly shown in investigations already published [3], whilst the negative kathodic after-current, which, under ordinary circumstances, is prominent in striated muscle, might be proved to be in the main a result of the alteration of the kathodic spots of fibre by the preceding closing excitation.

It is however intrinsically more difficult to attain a definite

[1] [This paper is the eighteenth in the series of 'Contributions to the general Physiology of Muscle and Nerve,' which have been published during the last six years by Professors Hering and Biedermann of Prague. Ed.]

[2] As I have since learnt from a copy of Professor Bernstein's Dissertation, 'De animalium evertebratorum musculis nonnulla,' Berolini, 1862, which he kindly sent to me, but which was unfortunately inaccessible to me at the time when I wrote my work upon the adductor muscle of Anodonta, he was the first to draw attention to the peculiar 'Tonus' of this preparation, and he had investigated its electromotive actions also before Fick.

[3] See No. VII and No. IX of this work. Also Hering, 'Über Veränderungen der Muskeln,' &c. Sitzungsber, vol. lxxxviii. p. 415.

conception in regard to the cause of the negative anodic and positive kathodic after-currents, especially as both phenomena, as will be shown, appear distinctly in striated muscle, only under certain conditions. It seems that here, certain subsequent phenomena of electrical excitation of tonically contracted muscles must be taken into consideration in the first place; these do not constitute excitation phenomena in the ordinary sense, i. e. phenomena of contraction, but much rather their opposite, that is, as relaxation of previously contracted parts, caused by an *inhibition of excitation.*

In this connexion I will only call to mind the phenomena of inhibition which result on electrical excitation of the muscle of the heart in systolic contraction, and which are so easily demonstrable and at the same time so remarkable. In studying these, one is necessarily led to the assumption of two processes antagonistic to the polar phenomena of excitation which I have denoted as 'inhibition of closing and opening,' or 'anodic and kathodic inhibition,' because the former has its origin at the point of entrance of the current, and the latter at its point of exit[1].

I further called attention to the fact, that if we assume a persistent tonic condition of excitation, then the result of the electrical excitation of such a muscle in respect to the secondary electromotive phenomena, must necessarily manifest itself under the circumstances, as a positive kathodic after-current, that is to say as a negative anodic one. Thus the strong positive kathodic polarisation, which under fitting circumstances is observed uniformly on electrical excitation of the adductor muscle of Anodonta, in consideration of its very marked 'tonus,' would be also easily explained by the hypothesis of a kathodic opening inhibition. The legitimacy of this conception, with which moreover other facts stated in the work mentioned are in complete accordance, was nevertheless necessarily left doubtful, since I had not succeeded in demonstrating the existence of polar phenomena of relaxation in so unequivocal a manner in the object named, as I had done in the muscle of the heart. Still this circumstance could hardly be maintained as a fundamental objection, because the tonus of this preparation is as a rule so strong, that a local and not very marked relaxation might easily escape demonstration by means of graphical methods, and all the more as the changes of form follow only languidly and slowly.

My effort has since been directed to gain certain and infallible

[1] 'Über das Herz von *Helix pomatia*,' Sitzungsber, vol. lxxxix. p. 19.

support for the theoretical conception of the secondary electromotive phenomena of the smooth muscle of Anodonta, and especially of positive kathodic polarisation in it, by the investigation of objects better suited to the purpose.

As there is such a regretable want of suitable organs with smooth muscles, experiments on the heart, especially of invertebrate animals, seemed at first to promise a good result; they fail, however, chiefly on account of the small size of the object. The heart is moreover very little suited for experiments on polarisation by reason of the complicated course of the fibre. Thus the only thing left was to consider the possibility of artificially putting striated trunk muscles into a continuous condition of excitation, lasting for a sufficient time, and comparable to the 'tonus' of certain smooth muscles, and during this condition to investigate the changes of form resulting on electrical excitation on the one hand, and the secondary electromotive phenomena on the other. I have endeavoured to attain this end by poisoning with veratrine, and I will communicate the results of my experiments in this matter on the sartorius muscle of the frog, in the following paragraphs.

I must not omit to mention here, that at the suggestion of Professor Hering, I made experiments several years ago, upon the effect of electrical stimulation on muscles in persistent contraction; although I had repeatedly succeeded at that time, by closing an electrical current, in producing a perceptible relaxation in muscle preparations which had been previously put into persistent contraction by the action of vapour of ammonia, yet the results seemed too uncertain to permit of making further deductions from them.

2. Changes of form which muscle poisoned by veratrine undergoes when excited by a battery current.

Since von Bezold[1] first determined accurately the remarkable effects of veratrine upon striated muscle, they have been repeatedly the object of detailed investigations. Their main result is the theory that the extremely striking after-effect produced by every stimulus, however short its action, is founded solely on a changed condition of the substance of the muscle itself, and as Fick[2] thinks,

[1] 'Unters. aus d. Würzburger Laboratorium,' 1867.

[2] 'Arbeiten aus d. physiolog. Laboratorium der Würzburger Hochschule,' ii. Lieferung, 1873, p. 142 f.

depends probably upon an 'intensification of the process of excitation beyond the normal amount.'

It is unnecessary to give an exact description of the variations in the contraction curve caused by veratrine poisoning, because a detailed examination of them is found in many works, and I have nothing essentially novel to add. I shall therefore limit myself here to a brief discussion of the method of poisoning which showed itself best suited to my purpose in the course of the investigation. As it was of the first importance to me to obtain a strong contraction of the whole transverse section of the sartorius, and especially that this should last as long as possible, the most appropriate way seemed to be to poison the whole animal; thus the only question was to find the most suitable dose on the one hand, and on the other to determine the point of time which should be considered the most favourable for the preparation of the muscle.

The extraordinary sensitiveness of the muscle of the frog for minimal amounts of the poison introduced through the blood, made me refrain for a long time from using stronger doses, because I feared a too rapid decrease of excitability. However, in the end, the use of larger amounts with a shorter period of action proved to be best. As some of the experiments took place at the beginning of the warm season, when the muscles of Rana esculenta are little suited on the whole for electro-physiological experiments as I had found from previous experience, I used later almost exclusively the muscles of R. temporaria. I had no ground for regret on this account, for they proved to be much more excitable, and are therefore better for the purpose than those of R. esculenta even at the most favourable season of the year.

Although, as Kölliker has already shown, a previous administration of curare is not sensibly prejudicial to the action of veratrine, I confined myself as a rule to the use of the latter poison alone, because certain appearances of movement which present themselves in the muscles of the poisoned animal, enable one to recognise the proper stage of the action of the poison with the greatest certainty. However, I assured myself every time by special control experiments, that the results of the experiments about to be described are in no way prejudicially affected by the simultaneous use of curare.

I introduced as a rule 6–7 drops of a 1% solution of acetate of *Veratrine* into the dorsal lymph sac, and killed the frog 10 minutes afterwards at latest. Generally 5–7 minutes suffice to produce

those symptoms, which, as already mentioned, characterise the proper stage of the action of the poison. Those which chiefly claim attention are more or less marked tetanic stretching spasms of the lower extremities, which succeed each other at rather short intervals, and are ushered in by violent restlessness of the animal and by spasmodic opening of the mouth frequently repeated. It must be considered the rule, to kill the animal before reflex movements are completely extinguished, and at a time when the heart still beats strongly and the circulation is in action throughout the body. The exposed muscles ought to be transparent and to show a good red colour. Another certain criterion of the fit state is, that the muscles of the belly pass into a state of long continuing tetanic contraction on mechanical excitation, such as nipping with the forceps. The same thing should also happen on dividing the nerve in preparing the sartorius. In doing this, it is often seen that after a short pause a more slowly increasing contraction succeeds the rapid twitching at the instant of the section of the nerve; this persists for some time and only gives way quite gradually to renewed relaxation. If the frog has been killed at a time when voluntary movements have already ceased and reflex excitability is almost entirely extinguished, then as a rule the muscles are scarcely in a fit condition; they still react indeed with a tetanic contraction on excitation, but this has not the same long duration, as in an earlier stage of poisoning.

Certain effects of poison on striated muscles, e. g. the results of treating with solutions of potash or soda salts, can, as is well known, be almost removed by washing with an indifferent liquid. Now it is remarkable that this is not the case for veratrine, or at least not nearly to the same extent, whether it is introduced into the course of the blood or is applied directly to the muscle. This circumstance is of importance, because it is thus possible to repeat the experiments of excitation several times in succession on the same preparation, but for reasons to be discussed later, this can only be done between long intervals of rest, during which the preparation remains plunged in a solution of Na Cl, or must at least be kept moist with it.

If we record the change of form of the sartorius poisoned in the way described with veratrine, which may be effected by securing the ends of bone to which it is attached, either in the usual manner or by means of Hering's double myograph without the middle clamp, one of the two movable non-polarisable electrodes being fixed, curves

are obtained which are essentially the same, whether the excitation is effected by an induction-shock acting anywhere along the muscle, or by the shortest possible closure of a battery-current in either direction. In both cases, the wave of contraction remains, so to speak, arrested on its way through the muscle and produces tetanus which continues for a longer or shorter time at about the same strength. When we consider the hitherto complete absence of proof of the discontinuous nature of this contraction, it will be better to describe it as a 'tonic' shortening of the muscle in all its parts.

As von Bezold and Fick have already remarked, various forms of the contraction of veratrine muscle can be distinguished, of which I mention only one of those of most frequent occurrence, viz. that in which the proper tonic persistent contraction is preceded by an initial twitch of short duration. In this case, just as I have described after section of the nerve, there occurs at the moment of excitation a rapid contraction of the muscle to a maximum; this is immediately succeeded by a considerable elongation, followed closely by another slow contraction which gradually gives way to relaxation.

I have hardly ever failed to observe indications of this characteristic mode of shortening, especially after the preparation has lain a long time in dilute solution of common salt. As Fick has already shown, it is out of the question to explain the initial twitch mentioned, by an indirect excitation of the muscle through the intermuscular nerves, and to refer the succeeding persistent contraction to direct excitation of the muscle exclusively; for just the same forms of curve are observed after previous curarising. The phenomenon may possibly be accounted for by what Grützner[1] has recently asserted as to muscle being composed of two kinds of fibre, morphologically and physiologically different, corresponding to red and white muscles. We may perhaps consider as in support of this view, the fact that the same sort of contraction-curves with two apices are not unfrequently observed under other circumstances e. g. after treating locally with Na_2CO_3, or even in quite normal curarised muscles. Grützner[2] goes so far as to believe, that such curves represent the rule for the fresh sartorius of the frog.

The form of shortening just discussed does not seem the most favourable for the experiments to be described. A more suitable form is that in which the contraction, at first rapid, is gradually

[1] Recueil zoologique Suisse, vol. i. No. 4 (zur Anatomie u. Physiol. quergestr. Muskeln).

[2] *Loc. cit.* p. 675.

retarded, and in which the gradually increasing relaxation is deferred for several seconds.

If in such a case, after the maximum of shortening has been reached, a battery current of medium strength (say two Daniells) is closed for 1–2 secs., especially if it be ascending, there is observed almost without exception an elongation of the muscle which is sometimes rather considerable. This elongation coincides in time with the moment of closure, and betrays itself by a sudden steep fall of the curve. Whilst the closure lasts, the curve either continues horizontal or shows a slight inclination towards the abscissa, and falls again more steeply only after the current is opened. It is the exception under these circumstances, to observe on opening the exciting current, a feeble renewed rising of the curve as an expression of the opening excitation of the muscle.

If the current is closed at a time when the muscle is no longer at its maximum shortening, then as a rule, a more or less evident closing contraction is observed. If the same excitation is repeated, by closing the current for a short time in unchanged direction at different phases of the shortening and renewed lengthening of the muscle, it is then seen that its proneness to excitation at closure is generally diminished in proportion to the degree in which it is shortened at the time of excitation. But even the completely relaxed muscle immediately afterwards scarcely responds to the same stimulus which shortly before produced a powerful contraction. In the majority of cases, however, the increase of the results of closing excitation keeps pace exactly with the gradually increasing relaxation of the muscle, so that closing twitches produced during relaxation at equal intervals, which almost always pass away rapidly, all rise to the same height above the line of descent of the curve which the muscle would have drawn had it been only once excited. Fick also made analogous observations of a frog's muscle poisoned with veratrine, by indirect excitation through the nerve, and I shall return to these presently.

If we observe more closely a veratrine muscle when in persistent contraction during electrical excitation, we easily see that the above described relaxation revealing itself in the curve by an almost rectangular descent when the current is closed, constitutes essentialy a local phenomenon, and indeed one confined to the immediate neighbourhood of the anode, with which moreover the small amount of descent in comparison with the total height of the curve is in agreement.

This fact may however be established with greater certainty and in a more complete manner with the aid of the simple artifice

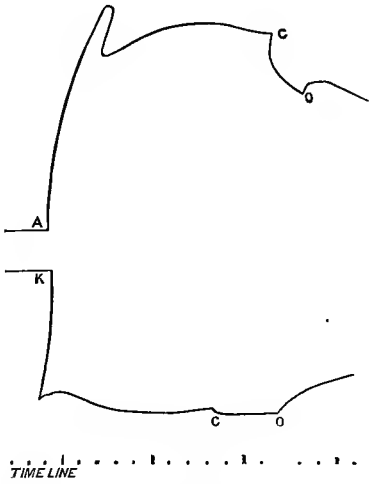

Fig. 8.

Fig. 8 represents the effect of exciting the *M. sartorius* of *Rana temporaria* after previously poisoning it with veratrine. A single Daniell was always used as the source of the current; a rheochord was not inserted in the circuit. The muscle was stretched in Hering's double myograph, and it was fixed at the middle. The tracing A is that of the anodic, and K that of the kathodic half of the muscle. Before the special excitation (at C), a tonic contraction of the muscle, lasting a long time, was produced by closing a battery current as short a time as possible, or by a single induction shock. The moments of closing and opening the exciting current are marked by the letters C and O. Its direction was ↓. In order to economise space, the tracings are shortened in such a manner, that the descending part corresponding to the renewed lengthening of the muscle is only reproduced in part. The phenomenon that the kathodic half of the muscle, on opening the current, is suddenly more relaxed, whilst the anodic half is either shortened or shows no alteration in length, is especially clear here. Both halves of the curve show at C and O exactly opposite changes of form. The divisions on the Time Line indicate seconds.

of fixing the muscle in the middle in such a way, that while the propagation of the excitation is unhindered, the variations in form of the one half are prevented from affecting the other. In doing this, I employed the same method which has already been discussed in detail in an earlier communication[1] and I need not therefore give a minute description of it here.

[1] Hering, 'Über die Methoden zur Untersuchung der polaren Wirkungen des elektrischen Stromes,' &c. Sitzungsber. vol. lxxix.

The phenomena which I hoped, vainly however, to show on electrical excitation of tonically contracted muscle of Anodonta, appear under these circumstances with convincing clearness in a frog's sartorius poisoned with veratrine.

If the muscle is fastened with proper precaution in a completely relaxed condition in the double myograph, and the middle is fixed with great care between oil clay, and if a single induction-shock of corresponding strength is sent either through the whole length of the muscle or through only a part of it, then, as a rule, both halves are nearly equally shortened, and the attached levers (one upwards and the other downwards) draw curves, which, except as to differences in size, are in every respect similar to those of freely twitching muscle described above. If, whilst the muscle continues at its maximum contraction, a battery current of sufficient strength is closed in the ascending direction, the anodic half is seen to lengthen considerably at once, the curve corresponding to it rapidly sinking, whilst as a rule, the kathodic half of the muscle shortens a little more, or undergoes no perceptible change in length. If now after the closing has lasted a short time, the current is again opened, in a successful experiment, exactly the opposite changes of form present themselves. The anodic half now shortens to an often not inconsiderable extent, this contraction being obviously the expression of the opening excitation, whilst at the same time the half corresponding to the kathode is distinctly more relaxed than would have been presumably the case had it not been stimulated. If the excitations are rapidly repeated with the same direction of current, the same phenomena, though diminishing in amount, appear as at the beginning of the experiment, provided that the muscle is still shortened to a considerable extent. A fact mentioned above repeats itself here, viz. that the readiness of the kathodic half of the muscle to respond to the excitation of closing, does not always increase in proportion to the progress of relaxation; it often indeed seems actually diminished, when the muscle has already regained its original length. After a longer pause however, the original excitability is recovered again without exception, and thus one is in a position to repeat the experiment several times in succession on the same preparation with like results.

It is hardly necessary to remark, that nothing essential is changed in the preceding experiment, if from the beginning, one excites with a descending instead of an ascending current, except that in the

former case, the effects of the excitation on the anodic half of the muscle seem less marked than those on the side of the kathode; this may be attributed in the main to the greater density of the current at

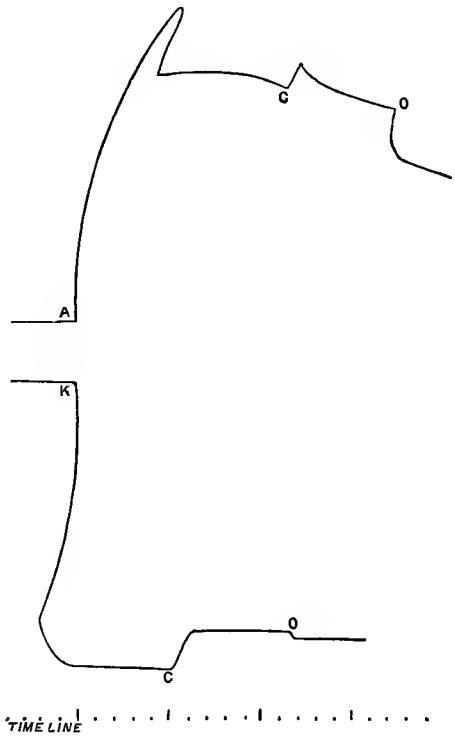

Fig. 9.

Fig. 9. Tracings obtained in the same way as in Fig. 8 when the exciting-current was directed ↑.

the point of exit. The sudden relaxation of the kathodic half of the muscle on opening the current is then shown with extreme distinctness and is recognised at once as a phenomenon equivalent to the anodic inhibition of closing.

From this description of the variations in form which are observed when a veratrine muscle in tonic contraction is excited electrically, and from a consideration of the examples of the curves which are given, we perceive at once that we are dealing here with essentially *local* changes of the muscle, confined to the immediate neighbour-

hood of the 'physiological kathode' and 'anode' respectively, and that these experiments give no information as to the possible extension of the changes beyond the place of their direct origin.

As far as my experiments hitherto go, it seems however that a propagation of the excitatory inhibition does not take place to any great extent in the circumstances under consideration, either from the anode (on closing) or from the kathode (on opening) the exciting current; the possibility of such a propagation is nevertheless not to be denied, for instances in favour of it actually exist. (Compare my observations on the muscle of the snail's heart.)

The relaxation of the kathodic end of the muscle, which occurs simultaneously with the opening of the excitation current, explains also the above-mentioned inhibitory after-effect of the electrical excitation of the muscle when not fixed in the middle, in case the opening excitation at the anode is inconsiderable. For it is obvious that the nature of the variation in form of the whole muscle at the opening of the current is conditioned solely by the mutual relations of the two antagonistic variations at the poles. If the kathodic opening inhibition preponderates, as is the rule when a muscle is much shortened, then a rapid further elongation must result on opening the current, and this constitutes apparently an after-effect of the anodic closing inhibition, which is usually more marked.

It follows hence directly, that a complete knowledge of the way in which the above-described mechanical results of excitation of persistently shortened muscle are in conformity with law, can only be gained with the help of the double myograph, and by using the artifice of fixing the muscle in the middle.

I do not, I think, go too far in regarding the variations of form of a sartorius thrown artificially into a 'tonus-like' condition by veratrine, as a complete counterpart of phenomena which I discussed as resulting from electrical excitation of the systolically contracted cardiac muscle. Here as well as there, besides the usual polar phenomena of excitation, which certainly appear less clearly than during the condition of rest and under some circumstances are suppressed altogether, polar processes of inhibition may be also directly demonstrated; these manifest themselves by the cessation or the diminution of an already existing condition of excitation and a relaxation of the muscle conditioned thereby,

which is primarily local. The elongation which takes place in a muscle which is in the state of persistent opening contraction, when the current is closed in the same direction as before, has been long known to occur, and must certainly be considered as a kindred phenomenon; the only difference is, that the question here concerns the inhibition of a condition of excitation produced at the physiological anode, by the after-effect of the current previously flowing through the muscle.

Notwithstanding the great sensitiveness of the veratrine muscle in repose, to the closing excitation, yet in general this excitation develops effects so much the feebler as the muscle remains more forcibly contracted at the time of excitation; now and then, after the return of complete expansion, it fails to produce any effects. Considering these facts, there seems in this behaviour a further analogy with systolically contracted cardiac muscle, and especially with the tonically shortened muscle of Anodonta. In the case of the former, Marey[1] showed that it is during systole quite unexcitable by feeble stimuli which are capable of exciting the diastolic heart to contraction, and that this excitation occurs the more readily the later the stage of relaxation in which it acts. This recalls directly the observation of Fick[2], already mentioned, that in indirect rhythmical excitation of a veratrine muscle in persistent contraction, all the twitches produced by it 'rise to very nearly the same height,' so that all their base points lie in a curve, which, as it appears, corresponds closely to the gradual re-expansion of the muscle after the first twitch.

In regard to the adductor muscle of Anodonta which consists of smooth fibre cells, I have myself found, that in a state of tonic contraction, it does not react sensibly even on very strong closing excitation, although on opening the current it sometimes contracts vigorously. On the other hand, when it is as much as possible relaxed, it behaves in regard to the current (leaving out of consideration the difference of period of the contraction) exactly like a normal striated muscle, for then the sensitiveness to the closing excitation is far greater than to the opening one.

The facts already mentioned appear to speak very decidedly in favour of the assumption, that in regard to the phenomena resulting from electrical excitation, far-reaching analogies exist between striated muscles of the trunk thrown into persistent contraction

[1] 'Physiologie expérimentale (Travaux du laboratoire de Marey,' 1876, p. 63 f.).
[2] *Loc. cit.* p. 146.

by veratrine on the one hand, and the tonically shortened adductor muscle of Anodonta and the systolically contracted heart on the other. This assumption is further materially supported by the agreement which, as will be shown, exists in regard to secondary electromotive phenomena, between the muscle of Anodonta and striated muscle poisoned with veratrine.

3. The secondary electromotive phenomena of veratrine muscle excited electrically.

Du Bois-Reymond[1] has already occupied himself with the experimental solution of the question, how the polarisation phenomena of striated muscle behave during tetanic excitation, and arrived at the result, that 'tetanised muscle undergoes less strong (positive) polarisation than muscle in repose.'

I also now directed my attention to the investigation of the secondary electromotive phenomena of a muscle tetanised through the nerve, and I selected the sartorius as the object presumably best fitted for the purpose. However I soon became convinced that satisfactory results are hardly to be expected in this way, because it proved that as a rule, the strength of tetanus is maintained at the same point, too short a time to allow of experimenting with sufficient certainty. Moreover it seemed desirable to replace the discontinuous tetanus by a more constant condition of excitation comparable to tonus, and I therefore had recourse again to the means of poisoning with veratrine already tried.

The method of poisoning the entire muscle through the circulation had proved best adapted for the investigation of the variations of form on electrical excitation, but it is less fitted in a case like the present, when the results of the excitation have to be examined by means of the galvanometer. The chief reason for this is, that the force of the excitation, as well as its period of passing away, are presumably not quite the same at all points, and hence there will be differences of tension in the continuity of the muscle; these do not admit of being estimated, and make it impossible to interpret the result of the observation with certainty in each case. I have therefore since adopted exclusively local poisoning of the muscle by direct application of a correspondingly

[1] See No. V. of this work.

dilute solution of acetate of veratrine, and by this method I have attained quite unequivocal results.

Before I proceed to state these results, I will briefly mention the experimental means which were available for my experiments. I had at my disposal a new large reflecting galvanometer with bell magnets by Edelmann of Munich; this presents a very substantial advantage for the intended experiments, inasmuch as its extremely strong damping renders nearly perfect aperiodicity possible without the use of Hauy's bar magnet. The magnet comes to rest in little more than a second.

The bobbins of the Edelmann instrument have however, on account of their large dimensions and the great number of turns, a resistance much too considerable for the present experiments, and I therefore used in their stead two bobbins with a less number of turns, made after Professor Hering's design. Each of these consists essentially of a copper hemispherical cup with thin walls, and when the bobbins are as close as possible to each other, the cavities of the cups almost enclose the spherical damper; the wires are wound directly over these copper capsules, and thus the greatest part of the space which would be injurious, and which is left empty even when the Edelmann bobbins are in actual contact, is made of use; and at the same time the coils lie much closer to the magnet here than there, so that notwithstanding their smaller number, the sensitiveness of the instrument is considerably increased.

When I led off from the artificial transverse section of a sartorius and from a corresponding point at about the middle of the muscle, with the brush electrodes already mentioned, I observed on an average a deflection of 40–50 scale divisions when the scale was at a distance of about 2·5 metres. The sciatic nerve of a larger frog gave deflections of 5–8 scale divisions, when led off from a tract about 1 centim. long under similar circumstances.

This amount of sensitiveness proved to be quite sufficient to demonstrate with all the certainty desirable, electromotive effects even much more insignificant than those concerned in the experiments which are about to be described. At the same time, the instrument offers the advantage which ought not to be underestimated, that the rapidity with which the magnet obeys the directing forces, makes it possible to recognise differences of tension which change their signs very quickly.

I may refer to previous communications for all the rest of the arrangements for the experiments, because they agree precisely

with the description given there[1]. However, I was able here, as well as in the polarisation experiments on muscle of Anodonta, to dispense with the use of the pendulum rheotome, because the closing time of the exciting current must not be allowed to sink below a limit attainable with the aid of a double switch, if the effects to be described are to come out with sufficient clearness. A more exact determination of the transmission time in each case is of no importance in the experiments now under consideration. Battery currents were used exclusively for excitation, and as a rule I employed two Daniells as the source of current.

I have already shown in an earlier communication[2], that by the direct action of properly dilute solutions of acetate of veratrine in 0·6% solution of common salt, it is easy to induce a locally limited condition of the muscular substance, which is identical with that observed in the muscles in their totality when the whole animal is poisoned, and this behaviour serves to make the law of polar excitation by the electrical current directly evident. I also called attention later[3] to the sometimes extraordinarily strong 'action current' which may be observed after momentary excitation at any point of a muscle which has been partially treated with veratrine, when the leading off electrodes are applied to the poisoned end of the muscle and to some point of the longitudinal surface higher up. The difference of tension to which this is due is, as I then found, very persistent, and under any circumstances lasts longer than the visible local persistent contraction of the muscle.

For the present object, which is solely concerned with the investigation of galvanic changes occurring under the influence of an electrical current in a length of muscle alternately in repose and excited, it was therefore an essential preliminary condition to make the negativity of the latter last as long as possible as an expression of excitation, in order to be able to carry out at least one polarisation experiment during this time. For this purpose a special method of local poisoning is required, and as such, I recommend the following mode, which hardly ever fails if the preparation is of sufficient sensitiveness.

As in the experiments described in paragraph 2, I used here also almost always the sartorius of *R. temporaria*, and as a rule I first poisoned the animals with a strong, quickly-acting dose of

[1] Sitzungsber. vol. lxxxviii. [2] *Loc. cit.* vol. lxxx.
[3] Sitzungsber. vol. lxxxi. p. 107 (Biedermann).

curare, without however discovering any difference when the curare was dispensed with. The muscle, with the two stumps of bone left attached to it in the usual way at both ends, was then stretched immovably in a horizontal position before it was excited: the lower thin end had been previously dipped up to about 5 mm. of its length for 5 to 10 minutes in a 0·6% solution of common salt, in which 0·01–0·03% of acetate of veratrine had been dissolved.

It is of special importance in these experiments to make it a rule to choose only preparations, the muscles of which look intensely red, as otherwise one cannot count on perceiving the phenomena resulting from the excitation with complete and convincing clearness.

When the end of the muscle is dipped into the solution of veratrine, contractions occur generally after a time; these are best prevented by a slight weighting of the muscle as it hangs vertically, so as to prevent other points of the surface besides the tract which is immersed from coming into contact with the solution.

Notwithstanding the fact that the veratrine solution is so very dilute it may still act so as to excite the muscular substance chemically, bringing about a persistent contraction of the immersed tract of muscle which often lasts after the time of immersion and occurs even in the best preparations. In this case, by leading off from the lower end and a point corresponding to about the middle of the muscle, a strong ascending action current is at once observed and it only gradually passes away. To exclude this, and also for reasons which shall be given later, I found it advisable not to make the polarisation experiment directly after removing the muscle from the solution, but only after leaving it for some time ($\frac{1}{4}$ hour and longer) in a physiological solution of common salt.

As I have already remarked, the very characteristic action of veratrine, in contrast with the changes effected in muscle substance by treating locally with potash or soda salts, is not removed even after long continued washing with indifferent liquids, but persists in almost unchanged strength until the death of the muscle, whether it is poisoned as a whole or only locally. If the muscle has not been injured in the preparation, and if the negativity, occurring as a result of whatever persistent contraction of the veratrinised part there may be, has been got rid of by leaving it for some time in a 0·6% solution of common salt, then, provided that the muscle has been very carefully stretched out, no appreciable differences of tension can be observed between the poisoned

end and the middle of a muscle, none at all events which the galvanometer is capable of showing. If the exciting electrodes are now applied to the bones at both ends, and the current of two Daniells is closed for a very short time in a descending direction, so that it traverses the whole length of the muscle, then if the galvanometer circuit is closed directly afterwards by turning the switch, there results a very strong deflection in the direction of a current opposed to the polarising one. The intensity of this current is always incomparably greater than that of a negative kathodic polarisation current which appears in normal muscle preparations under similar conditions but after a much longer period of closure. It even exceeds that of the demarcation current.

It can hardly be doubted that this difference of tension is caused by the strong and protracted excitation of the tract of muscle which has been treated with veratrine, and the current produced by it must accordingly be considered as an 'action current.'

The development of this current, as regards time, very frequently results in such a manner (and these are exactly the most favourable cases for the following experiments) that immediately after opening the exciting circuit and closing that of the galvanometer, the deflection attains a certain amount very quickly, remains constant at this amount for a short time, and then increases gradually during several seconds, until finally it passes away slowly. If now, after compensating as quickly as possible, the excitation is repeated with a descending current in the same way as before, whilst the position of the magnet remains unchanged or is still in the act of increasing, *then, without exception*, there follows *a more or less considerable backward swing*, indicating a polarisation current which has the same direction as that of the stimulating current, and is therefore positive. The image of the scale then either returns to its former position more slowly, sometimes passing beyond it, or it takes up a new position, which indicates a persistent diminution of negativity of the fibres at the kathodic spots.

Whether the one or the other happens, depends essentially upon the stage of the development of the action current when the excitation takes place. If the polarising current is closed immediately after it begins or only a little later, then after an excitation of short duration, the diminution of the negative after-current caused by it, is seen almost uniformly to be succeeded by a corresponding increase; and the same experiment can be repeated several times in succession with the same result. If however the excitation

takes place at a time when the spontaneous decrease of the after-current is imminent, or has already begun, then as a rule only a more or less considerable and sudden acceleration of the return is effected; if the excitation takes place later still, negative polarisation is again produced, although it is much feebler than at the commencement of the series of experiments. Sometimes in this case also, the opposite positive action becomes still perceptible by a transient delay of the negative deflection.

It is noteworthy that if directly after the passing away of the action current, which always takes a rather long time, the same descending current, which at first produced such powerful effects, is closed, only comparatively trifling deflections in the direction of a negative polarisation current are obtained. If however, the muscle has a longer period of repose, being left in a physiological solution of common salt in the interval, then on the same excitation exactly the same phenomena described above are repeated. This is very much in favour of the assumption of a local fatigue, caused by the strong and prolonged state of excitation of the poisoned part of the muscle; and another fact is in accordance with it, viz. that the mechanical results of excitation under the same circumstances often seem to be seriously impaired.

The following tabulated results of experiments will serve to explain the foregoing more clearly.

The horizontally stretched muscle is to be supposed throughout as having its lower end turned towards the left; two out of the three galvanometer electrodes were in direct contact with the tendinous ends, and the third was in contact with a corresponding point of the middle of the muscle. The exciting electrodes were applied to the two stumps of bone. The leading off was as a rule only from the left kathodic half. The direction of the polarising current is indicated in the tables by arrows.

1. *Rana temporaria*, curarised, the lower end of the sartorius dipped in 0·01% solution of veratrine for 5 min., afterwards treated with 0·6% Na Cl. solution for 15 min. Cl. T = closing time. M. St. = momentary stimulation effected by a rapid closing and opening of the exciting circuit by means of the double switch. Before the first stimulation, the muscle is found to be without current on leading off from the kathodic half. The strong negative action current after the first, fifth, and ninth excitations is rapidly compensated every time.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	quick to −40, slow to −74 sc.		
„	1 sec. ←	+18, quick to 0		
„	2 „ ←	+32, „ +4		
„	4 „ ←	+9, „ 0		
				After a pause of 10 min. M. C. (muscle current) = −8 sc.
2 Dan.	M.St. ←	−32, slow to −56		
„	2 sec. ←	+32, quick to 0		
„	2 „ →	+16, „ −8		
„	2 „ ←	+24, „ +3		
				Pause of 10 min. M. C. = −7 sc.
2 Dan.	M.St. ←	quick to −24, slow to −47		
„	1 sec. ←	+26, slow to −2		
„	3 „ ←	+8, slow to 0		
„	5 „ ←	−12, slow to 0		

2. *Rana temporaria*, curarised; everything as in the previous experiments.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	quick to −21, slow to −54		
„	M.St. ←	+12, slow to 0		
„	1 sec. ←	+23, slow to −5		
„	3 „ ←	hesitates then −3		
„	5 „ ←	−14, slow to −6		
				Pause of 15 min. MC. = −12 sc.
2 Dan.	M.St. ←	quick to −18, slow to −35		
„	1 sec. ←	+20, slow to −2		
„	3 „ ←	−8 +15, slow to 0		
„	4 „ ←	−18, slow to −12		
				Pause of 10 min.
„	M.St. ←	quick to −25, slow to −39		After crushing the lower (left) end of the muscle and compensating the current.
„	2 sec. ←	+24, slow to −5		
„	2 „ ←	+36, slow to +3		
„	2 „ →	+28, slow to +10		

Thus, as is directly proved from the preceding series of experiments, strong positive kathodic after-currents may be observed

in striated muscle when excited by battery currents under suitable conditions. It appears to be essential that the spots of fibre, which represent the physiological kathode, shall be already in a uniform state of strong excitation at the moment they are stimulated, and this is obviously in complete accord with the theoretical views already mentioned.

It might be advanced as an objection, that the question in these experiments is not so much that of a kathodic opening inhibition comparable to the anodic closing effect, but rather that of the result of a local fatigue of the muscle, due to previous excitation at the points of exit of the current, the fatigue having enfeebled the already existing excitation transitorily or permanently. Against such a view however the fact speaks decisively, that the magnitude of the positive deflections throughout does not increase in proportion to the duration of closure of the polarising current, as would certainly be the case if the relative positivity of the kathodic points of the fibre were conditioned only by a local fatigue.

Thus a glance at the tables before us shows that an increase of the positive kathodic effects with increasing duration of closure, takes place only within very narrow limits and soon changes to the opposite, although the tonic excitation still exists in sufficient amount, and therefore excitations of short duration are succeeded afterwards as before, by positive deflections. It is often possible to observe that when the duration of closure is gradually increased, the deflections which were at first entirely positive, next become diphasic (positive deflection with a negative preceding it); finally the second phase gradually diminishes, until at last it gives way to effects wholly negative in direction (comp. Table 2).

It is quite as much out of the question to explain the positive kathodic after-current by an opening excitation propagated from the anode up to the middle electrode of the galvanometer. Any such assumption is seen from the first to be inadmissible, when we consider the comparatively slight strength of the exciting current, combined with the short time of closure, and the fact that the descending direction of the current is unfavourable for producing strong opening excitation of the sartorius. It is however easy to convince oneself in every case, that on leading off in the continuity of the muscle, at about the middle third, no considerable differences of tension are to be found under the given conditions of experiment.

Thus, so far as I see, the hypothesis already mentioned alone remains, viz. that *at the moment of opening the exciting current*, an

inhibition of the state of excitation already existing at the physiological kathode develops itself, giving rise to relative positivity of the kathodic spots of fibre, and that in the case now before us, the positive kathodic after-current is conditioned by this inhibition.

The experiments in regard to the variations of form of electrically excited veratrine muscle, spoken of in the second section of this paper, stand in perfect agreement with this interpretation of the observed phenomena. It accords no less completely with facts which remain to be described.

As already frequently mentioned, the resulting phenomena of the changes of the stimulated muscle substance, produced under the influence of the anode whilst the current remains closed, resemble in every respect those observed under the same circumstances at the kathode on opening the current. This holds good, not only with regard to the variations in form of the muscle, which may be characterised in both cases as a locally limited relaxation, but also in regard to the accompanying electromotive phenomena which are characterised by the relative positivity of the point of entrance or of the point of exit of the current, and give rise in the one case to a negative anodic, in the other to a positive kathodic after-current.

Since the method of the investigation of secondary electromotive effects only permits of determining the results of electrical excitation *after opening* the polarising current, it is clear, that as soon as the conditions for producing distinct opening excitation are given (especially when stronger currents and longer period of closure are used) the positive anodic after-current caused thereby will come into prominence, whilst the negative after-current can only sometimes make itself apparent as a preliminary jerk. Only in the case in which the accomplishment of the opening excitation is impeded in any way, or is altogether prevented, can one expect to observe stronger effects in the direction of a negative anodic polarisation current, as e. g. is actually the case with exhausted preparations, or after the anodic ends of fibre have been killed. In this connection, it is of interest to notice that under the same circumstances in which on opening the current, strong kathodic effects are observed in the sartorius veratrinised at one end, negative anodic after-currents are also found to exist if the current enters at the poisoned end of the muscle, and this happens under conditions in which in normal preparations, purely positive anodic polarisation of considerable strength might have been expected to present itself. (Comp. Tables 1 and 2.)

It is further very remarkable, that *the positive kathodic polarisation in muscles veratrinised at one end is not only not impaired by killing that end of the muscle during the existence of the state of excitation there, but, as I had also previously observed in the muscle of Anodonta, it very often increases considerably.*

Even directly after an action current produced by a momentary excitation has passed away, it is possible at once to renew its power of giving positive kathodic after-currents, in a muscle prepared in the manner indicated. This may be done by killing the poisoned fibre ends corresponding to the point of exit of the exciting current, by crushing them with the forceps and compensating the strong demarcation current produced thereby. By this procedure it is well known that the production of a closing excitation is materially prevented, while, as it appears, the results of the inhibitory actions come into play as strongly after as before. However, before I consider in detail the meaning of this phenomenon, which is surprising at first sight, I must discuss some other facts which relate to the existence of positive kathodic after-currents on exciting electrically normal muscles that have not been poisoned.

4. Positive kathodic polarisation in normal striated muscles.

Hering[1], who used exclusively muscle of *R. esculenta*, mentions that sometimes in quite fresh muscles after the first excitation, extremely feeble deflections of the magnet occur in the direction of a positive kathodic polarisation, but he did not proceed to a more detailed investigation of these trifling effects at that time. Since then, on repeating similar experiments on preparations of the sartorius of frogs (*R. esculenta*) which had been cooled in ice, and the excitability of which had attained a very high degree, I succeeded several times in getting stronger positive kathodic effects, but they are still far less considerable than those which may be observed under similar circumstances in preparations of *R. temporaria.*

Thus, on using the Edelmann galvanometer I was surprised that normal sartorius preparations of *R. temporaria*, on being excited with currents of medium strength and short period of closure, and on leading off from the lower (kathodic) end, and from a corresponding point of the middle of the muscle, gave at first very often exclusively positive kathodic after-currents of considerable strength.

[1] Sitzungsber. vol. lxxxviii. p. 430.

The deflections, which I observed in the most favourable case under these circumstances, never amounted to more than a few (at most five) scale divisions; still there could hardly be any mistake about it, as all sources of error were excluded, and it only remained to make the feeble effects more clearly perceptible, by using an instrument so delicate as to make a more exact investigation possible.

I will give first of all some values of positive kathodic polarisation observed in a fresh, not poisoned sartorius of *R. temporaria*, when the Edelmann galvanometer was used, in order to compare them with the earlier experiments on veratrine muscle.

3. Arrangement of experiments as in 1 and 2.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←—	+ 5 sec. slow to 0	}	
,,	,, ←—	+ 2 ,, ,, 0	}	
,,	2 sec. ←—	−14 ,, ,, −3		
,,	M.St. ←—	+11 ,, ,, 0	}	After crushing the lower (left) end and compensating the current.
,,	1 sec. ←—	+ 4 ,, ,, 0	}	
,,	3 sec. ←—	−12 ,, quick to +1	}	

In all the experiments which will be described in the following paragraphs, I used a mirror galvanometer constructed by Meyer of Zurich after Hermann's specifications, and which left nothing to be desired as regards sensitiveness. I refer for a description of it to Hermann's paper in Pflüger's Archiv[1] and will only remark that the new instrument used by me has 1000 turns more than that of Hermann. The current from the longitudinal to the transverse section of the sciatic nerve of a medium-sized frog with its lower end lying on the brush electrodes, produced on an average, a deflection of 120–150 scale divisions when the instrument was made aperiodic by Hauy's bar magnet, the leading-off electrodes being about 1 cm. apart and the distance of the scale from the mirror about 2·5 metres. The demarcation current of the sartorius, when similarly led off, naturally drove the scale at once far out of the field; consequently whenever there were any considerable differences of tension at the beginning of the experiments of excitation, it was necessary to adjust the compensator approximately before closing the galvanometer circuit.

[1] Pflüger's 'Archiv,' vol. xxi.

Under these circumstances it could be shown with complete certainty that *positive kathodic polarisation is a consequence of electrical excitation with battery currents even in striated muscles which are entirely uninjured. Under favourable conditions this can be always demonstrated.*

In proof of this statement I give the three following series of experiments, which require no further explanation to be understood.

4. Sartorius of *R. temporaria* curarised. The arrangement of experiment is as in 1, 2, and 3. The sign > denotes that the image of the scale moves back with decreasing speed. The muscle current of the left half amounted at first to −70 sc. and was compensated.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	+108 sc. > 0		
,,	1 sec. ←	+ 87 > 0		
,,	3 ,, ←	− 23+14 > −42		
,,	2 ,, ←	− 12+55 > −22		
,,	1 ,, ←	+260 > +50		
,,	5 ,, ←	+140 > +12		After crushing the lower end of the muscle. (MC. compensated.)
,,	10 ,, ←	+ 58 > +32		
,,	10 ,, ←	− 27+8		
,,	M.St. →	+ 226 > 0		

5. Sartorius of *R. temporaria* curarised. Arrangement of experiment as before. MC before the commencement = −76 sc.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	+53 quick −22		
,,	1 sec. ←	+36 ,, −30		
,,	2 ,, ←	−82 slow −18		Pause of ¼ hour. MC. = +82 sc.
,,	M.St. ←	+13 quick −11		
,,	1 sec. ←	−3+8 quick −15		
,,	1 ,, ←	+56 > +12		After crushing the lower end of the muscle. (MC. compensated.)
,,	3 ,, ←	−42 slow −24		

6. Sartorius of *R. temporaria* not curarised; the upper end of the muscle tied off, everything else as in the previous experiments. MC at the commencement -52 sc.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	$+48 > +2$		Pause of 3 min., MC. = 0.
„	M.St. ←	$+53$ quick $+9$		
„	„ ←	$+32$ „ -12		
„	1 sec. ←	-70 slow -24		
„	M.St. ←	$+52 > -43$		After crushing the lower end of the muscle and compensating the current.
„	1 sec. ←	$+35 > 0$		
„	2 „ ←	-5 slow -16		
„	1 „ ←	$+49 > 0$		
„	4 „ ←	-46		

An inspection of the preceding tables shows that the positive kathodic polarisation of uninjured muscles may sometimes attain to very considerable values; even if such powerful effects as e. g. in Table 4 are regarded as exceptional, we shall nevertheless scarcely ever fail to find after-currents of the kathodic half of the muscle, on excitations with battery currents of medium strength and of short duration, provided that the preparations are sufficiently sensitive. These after-currents either appear at once after closing the galvanometer-circuit, or are preceded by a more or less marked negative preliminary jerk, which sometimes only shows itself as a delay of the positive deflection. One may say in general, that the kathodic polarisation phenomena of fresh muscles depend upon the closing time of the exciting current in this sense, that as a rule at first only unmixed positive after-currents appear, with which afterwards negative ones are associated, increasing rapidly with the period of closing, so that whereas at first they present themselves as preliminary jerks, they subsequently entirely suppress the positive effects. Hence these latter sometimes, so to speak, look like a transitory 'positive variation' of a negative polarisation-current, after the expiration of which, the magnet swings again almost uniformly with decreasing velocity beyond the zero point, so that, finally, a more or less strong negative deflection remains behind, and this disappears only quite gradually. (See Tables 4 and 5, and below 7 and 8.) Sometimes the positive effect seems

to be indicated only by slight hesitation of the negative deflection. (See below, Table 8.)

Though kathodic polarisation in fresh uninjured muscles varies in some details as to its mode of manifesting itself, still under all circumstances, it is always easy to determine the fact that the intensity of the led-off positive after-current is directly dependent upon the time of closure of the polarising current, in such a way that it always decreases rapidly as the latter increases. Beyond a certain duration of closing time, a purely negative kathodic polarisation is observed without exception; and in less excitable preparations this is the case from the first. Positive kathodic polarisation also shows itself dependent upon the strength of the exciting current as well as upon the closing time. Very feeble currents, if they have any effect at all, produce always only feeble negative after-currents; and the same thing is true, on the other hand, of very strong ones, by which the muscle substance at the kathode is evidently subject to profound changes, even when the duration of closing is shorter.

Other facts which will be communicated later, support the idea that a certain relation exists between the positive kathodic polarisation current and the electromotive behaviour of the muscle in repose, of such a nature, that the current is more easily and more strongly developed if a normal current of repose is present from the very first; e. g. when, as in our case, the lower tendinous end is negative to the middle of the muscle. Although, however, on the ground of results which remain to be discussed, such a relation is not to be denied, yet it can by no means be held as a universal law; and therefore I desire to lay special stress on the fact that I have observed positive kathodic polarisation, not only in preparations which from the first showed normal differences of tension in the sense of an ascending demarcation current, but also in muscles wholly without current, as well as in those which were electromotive in the opposite direction.

If we look through a long series of polarisation experiments on fresh sartorius preparations of *R. temporaria*, as uninjured as possible, we cannot fail to see, that even if positive kathodic after-currents are observed in the majority of cases at the first excitations, yet as a rule these are essentially of inferior strength to the other secondary electromotive phenomena and particularly to the positive anodic after-currents. Cases like that mentioned in Table 3, of which I have observed several, are nevertheless

exceptions, at least at the season (early spring) when my experiments were performed. Later in the year, when the animals have been for a longer period in a higher external temperature, and their muscles no longer show that beautiful red tint which is so characteristic of their good condition, even slight traces of positive kathodic polarisation are only exceptionally observed.

Now it is very remarkable and of the greatest interest for the interpretation of positive kathodic after-currents, *that after killing the end of the muscle corresponding to the 'physiological kathode,' it is easy, even in less sensitive preparations, to observe tolerably strong positive after-currents when atterminally directed battery-currents are used for stimulation.*

A glance at the above Tables 4, 5, and 6 shows, that after the kathodic end of the muscle has been killed, positive polarisation at the points of exit of the current is just as possible here as in the veratrine muscle. In the majority of cases indeed a considerable strengthening of the + deflections took place after the injury. This justified the expectation, that in cases also where positive kathodic effects are not demonstrable at all, they might be produced, so to speak, artificially, by killing the kathodic end of the muscle. The following series of experiments show that this is in fact the case.

7. Sartorius of *R. temporaria*, curarised. Arrangement of experiment as before. MC = −20 sc.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	1 sec. ←	−6 + 14 quick to −25		
„	M.St. ←	−34 slow to −18		
„	M.St. ←	+83 > +2		Third and following excitations after crushing the lower (left) end of the muscle. Current compensated.
„	1 sec. ←	+112 > +25		
„	3 „ ←	+91 > +18		
„	5 „ ←	+24 slow to +11		
„	6 „ ←	−20 „ 0		
„	1 „ ←	+54 > +6		

8. Sartorius of *R. temporaria*, curarised. Arrangement of experiment as before. MC = +9 sc (reversed).

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	quick to −3 + 12 −15		
,,	M.St. ←	,, −7 hesitating then quick to −22		
,,	1 sec. ←	+76 > +8		The third and following excitations after killing the lower end by concentrated solution of Na_2CO_3. (MC. compensated.)
,,	5 ,, ←	−63 (lasting)		
,,	1 ,, ←	+66 > +12		
,,	1 ,, ←	+97 > 0		

9. Sartorius of *R. temporaria*, curarised. Arrangement of experiment as before. MC. before commencing = −43 sc.

Number of cells.	Cl.T.	Left half.	Right half.	Remarks.
2 Dan.	M.St. ←	−32 > −5		
,,	M.St. ←	+46 > −11		The second and following excitations after killing the lower end with concentrated solution of Na Cl.
,,	1 sec. ←	+23 > 0		
,,	3 ,, ←	−26 > +3		
,,	M.St. ←	+33 > −4		
,,	,, ←	+36 > 0		M. C. compensated (460°).
				After a pause of ½ hour.
,,	M.St. ←	−114 (lasting)		M. C. compensated (280°).
,,	,, ←	+24 > −2		

As the preceding series of experiments show, positive kathodic polarisation in a muscle of which the kathodic end has been killed, obeys exactly the same laws in regard to its dependence upon the intensity of the exciting current and its duration of closure as muscle veratrinised at one end, and, apart from differences of degree the corresponding phenomena accord throughout. The negative preliminary jerk, which often ushers in the positive kathodic after-current in normal uninjured muscles, is wanting in both cases throughout, a circumstance which, as it seems, makes the near connexion which doubtless exists between the kathodic closing excitation and the negative after-current, come out in clear relief.

That is to say, if the negative preliminary jerk is to be regarded as essentially an immediate after-effect of the closing excitation, then like this, it must be altogether or partially suppressed by killing at the kathodic end, as is in fact always the case. On the other hand, it was shown earlier, that also during the existence of a persistent excitation of the kathodic parts of the fibre of a muscle treated locally with veratrine, a battery current of corresponding direction produces only a feeble closing excitation or none at all.

If we take into account the very striking agreement which exists in regard to the conditions of commencement and mode of manifestation of positive kathodic polarisation in veratrine muscle on the one hand, and on the other, after the death of the kathodic ends of fibre in normal striated muscle, it certainly seems a very natural idea to refer the phenomenon to the same cause in both cases. Hence, here as there, we should have to deal with inhibition of an existing state of excitation, and with the consequent relative positivity of the points of exit of the current as compared with other points in the muscle, this inhibition being produced at the physiological kathode on opening the exciting current.

However little reason there may be to doubt the correctness of this conception as regards locally veratrinised muscle, the generalisation thus indicated requires a more complete justification.

It cannot be denied, that after killing at one end the terminations of the fibre of a normal regularly constructed muscle, the nearest excitable transverse sections of it are in a condition of more or less strong persistent excitation, and this betrays itself moreover often macroscopically by local contraction, but in all cases, it is easily recognised by means of the microscope.

But under this hypothesis, the occurrence of positive kathodic after-currents, when a muscle injured at one end is traversed by an atterminal current, is no longer surprising; for under the hypothesis of an opening kathodic inhibition, this is an immediate and necessary result which ought to follow the procedure to which it has been subjected. Such a preparation does not behave differently in any essential point immediately after a momentary excitation, from a muscle which has been treated locally with veratrine; and everything which has been previously communicated as to the behaviour of secondary electromotive phenomena in such a muscle can be applied directly to the case now before us.

In connection with the preceding discussion it is worth noticing that the way in which the end of the muscle is killed is not quite

a matter of indifference as regards the positive kathodic polarisation which results from the excitation. I observed the strongest positive kathodic after-currents uniformly, after the local action of concentrated solutions of soda salts (especially Na Cl. and $Na_2 CO_3$) on the kathodic end of the muscle. Mechanical injury by crushing has a decidedly feebler effect, and still more unsatisfactory is local treatment with dilute solutions of potash salts, by which the excitability is at once speedily and considerably impaired. It is well known, that the soda salts named, strongly excite the muscle substance at the commencement of their action, or at least increase its excitability. Now when they are applied locally, a slow distribution of the salt solutions takes place owing to diffusion; the first effect must therefore be to bring fresh sections of the muscle in the vicinity of the demarcation surface successively into a condition of excitation. It is evident that under these circumstances the conditions for the development of positive kathodic after-currents are most favourable. Thus it is precisely in the first period after killing the kathodic fibre ends by concentrated solution of common salt, when the demarcation current which it produces is still in the act of slow increase, that we usually see the strongest positive effects.

The capability of such a preparation of yielding positive after-currents which can be led off from the kathodic half of the muscle, under the given conditions, is moreover a very persistent one, and continues, though in diminished degree, even after prolonged washing with dilute salt solution. The muscle then (after a quarter to half an hour), on its electrical excitation, often shows a behaviour quite similar to that after local poisoning with veratrine: thus after a battery current, atterminally directed, has been closed for the shortest possible time, on leading off from the kathodic half, there is at first a very strong deflection in the direction of an increase of the (compensated) demarcation current, that is a negative polarisation, but a moment later, the same stimulus produces a more or less strong positive polarisation. (See above, Table 9.)

In all cases, in which after the death of the muscle at one end, positive kathodic polarisation prevails over negative kathodic with atterminal direction of the current, it can always be shown that with an abterminally directed exciting current, an exactly opposite reciprocal relation exists between the positive and negative anodic after-currents, the negative invariably predominating.

I hardly need to emphasise further, that in none of the cases before us were any considerable differences of tension in the con-

tinuity of the muscle within the interpolar tract observed as results of electrical excitation, so that it may be regarded as a firmly established fact, that the polarisation phenomena discussed are of exclusively polar origin. This is noteworthy, because otherwise it would be natural to consider the experiments on positive kathodic polarisation of striated muscles as supporting the views maintained by du Bois-Reymond as to the existence of an *internal* positive polarisability of muscle.

If, as I believe, we may maintain that we have in the main succeeded in referring to the same cause, the positive after-currents which are observed on the electrical excitation of locally veratrinised muscle on the one hand, and those in a muscle of which the kathodic fibre-ends have been killed on the other, there still remains the question to be answered, how positive kathodic polarisation of currentless muscles, which have been injured as little as possible is to be understood.

This ought not to be compared with the corresponding phenomenon in the uninjured muscle of Anodonta without further ground; for this latter is in a state of persistent excitation in all its parts, whilst normal striated muscle may be assumed to be in repose. If in the former case we are dealing only with the phenomena resulting from inhibition of tonic excitation appearing at definite spots, and a *relative* positivity of those spots caused thereby, then in the latter case it is necessary to assume a local change in the muscle substance in repose, which displays itself by its becoming positive in regard to other unchanged parts of the fibre. As is at once obvious, such a change at the kathode, under the existing circumstances, can be regarded only as a phenomenon consequent upon the preceding closing excitation, by which the same points of the fibre become without doubt first of all strongly negative, so that the idea immediately forces itself upon us, that we are dealing here, so to speak, with a reaction of the living substance against the preceding excitation.

It is not without interest for the study of the changes of muscle substance at the kathode, of which we are speaking, that we have it in our power in every muscle, by treating any portion of it with certain chemical substances, not only, as I formerly showed, to make it negative[1], but also positive as compared with other parts; and

[1] 'Über die Abhängigkeit des Muskelstromes von localen chemischen Veränderungen der Muskelsubstanz,' Sitzungsber. vol. lxxxi. p. 74.

in this way to produce artificially what may be called a reversed muscle current.

In the work just quoted, I mentioned experiments which I performed at that time with $Na_2 CO_3$ and other agents calculated to increase the excitability of muscle substance, in the hope that I might succeed in making by their local action, certain points positive in regard to others. The low degree of sensitiveness of the instrument, which alone was then at my disposal, an old Meyerstein mirror galvanometer, did not make it possible to answer the question decidedly.

I have recently resumed these experiments, and have convinced myself that after local treatment with dilute solutions of $Na_2 CO_3$, Na Cl, or veratrine, the differences of tension anticipated can be demonstrated very easily and with great certainty.

If the uninjured lower end of a sartorius is dipped for a short time (5–10 min.) in a 0·5–1% solution of $Na_2 CO_3$ (a 2–4% NaCl solution proves less efficient) it will be found more or less positive in regard to the middle of the muscle. Under these circumstances employing muscles that were previously currentless, deflections of + 200 scale divisions and upwards with the Hermann galvanometer which I used, were by no means of rare occurrence. Feeble normal currents are got rid of or even reversed. The (reversed) 'soda currents' may be again got rid of by a rather long washing with a physiological solution of common salt, though less easily than 'potash currents.'

Now, disregarding other differences, one very essential difference exists between the result, just discussed, of the direct action of certain chemical substances, and the positive kathodic polarisation which arises from the electrical excitation of uninjured currentless muscles. In the latter case, as has been already mentioned, it is obvious that we are dealing with an *indirect* effect of the current, with a 'Reaction' of the muscle substance from the primary process of excitation produced at the kathode. The chief fact in support of this is, that after a longer duration of closing or with less favourable preparations, a negative preliminary jerk often precedes the positive deflection, as was shown above, and that in less sensitive muscles (especially in those of *R. esculenta*) there seems to be only a trace of positive kathodic polarisation, or it is altogether absent. With reference to this, I must remark further, that the positive reaction at the kathode does not, as it seems, stand in direct dependence upon the condition of excitability of the kathodic

spots at the time, but on other, for the present unknown, conditions. Otherwise, after local treatment of the kathodic end of the muscle with dilute solutions of Na_2CO_3, by which excitability is enormously increased, we should expect to find, with a corresponding direction of current, positive kathodic after-currents in those cases also, in which previously no trace of them could be demonstrated. This is however never the case, the result of such a procedure being always merely to favour in a remarkable manner the negative kathodic and positive anodic polarisation (as expressions of the closing and opening excitations respectively), whilst positive kathodic and negative anodic after-currents do not appear even with the shortest possible duration of closure attainable by means of the switch. It still remains to be investigated, how the secondary electromotive phenomena would behave under the same circumstances, on excitation with induced currents. It must be left for further investigations to decide whether the positive reaction of muscle substance, which has been assumed here, is exclusively determined by electrical excitation and only occurs at the spot directly excited (the physiological kathode), or whether it may also be observed when other excitants are employed and at a distance from the excited spot namely in the continuity of the muscle, as if it followed the propagation of the wave of excitation.

The results at which I arrived, at the time of my investigations on the consequences of electrical excitation of the muscle of the heart (of the snail and of the frog) as well as of the adductor muscle of Anodonta, gain in significance from the fruits of the present work. For I am now in a position to generalise the conclusions to which I was then led by the observation of the effects of exciting the cardiac muscle when in different states of contraction.

The assumption of two processes of inhibition, antagonistic to the polar processes of excitation, which seemed to be incontestable for the cardiac muscle in the state of systole, now proves to be that which is capable of affording the simplest explanation of the phenomena following on electrical excitation of striated muscle.

The same thing is true for results of mechanical stimulation as for electromotive after-effects. The two methods of investigation, viz. the examination of the changes in form of the excited muscle on the one hand, and the determination of the condition of polarisation at the close of excitation on the other, mutually supplement each other in the desired way, so that a satisfactory insight into

the nature of the changes effected by the current is in fact to be attained only by the combination of both methods of investigation. In this connection it should be distinctly noticed, that a direct proof of the presence of an antagonistic process following or preceding excitation, and indicated by corresponding changes in form of the muscle, is obviously only possible in the course of a persistent contraction of the muscle which has already come into existence; without this, it could only be inferred in a most indirect way, by observations of the changes of excitability. On the other hand, the investigation of secondary electromotive phenomena serves to demonstrate with complete certainty, the existence of polar antagonistic processes in muscle when in a state of repose.

Positive anodic polarisation coupled with negative kathodic on the one hand, positive kathodic polarisation coupled with negative anodic on the other, owe their origin to polar antagonistic alterations of the muscular substance: one set of these alterations produces negativity and the other set produces positivity of the affected spots. The closing and opening contraction represent the mechanical excitatory effect of the former, and the opening and closing relaxation the inhibitory effect of the latter (when a tonic condition of contraction is present). Both contraction and relaxation are no doubt conditioned by chemical changes of the excitable muscle substance, evoked by the influence of the current, though nothing definite can be said at present as to the nature of these changes. But while the changes which take place on closing the current are directly produced by it, the effects of opening it are essentially reaction phenomena, which have their origin in the altered muscular substance; a statement which applies not only to the anodic opening excitation, but also to the kathodic opening inhibition.

PART III.

RESEARCHES

RELATING TO THE

ELECTRICAL ORGANS OF MALAPTERURUS

AND

TORPEDO.

XI.

OBSERVATIONS AND EXPERIMENTS

ON MALAPTERURUS BROUGHT TO BERLIN ALIVE.

By E. DU BOIS-REYMOND.

Gesammelte Abhandlungen zur allgemeinen Muskel- und Nerven-physik, vol. ii. p. 601.

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XI.

1. Introduction.

THE unusual interest which electrical fishes[1] have always excited, has been increased still further at the present day, by its becoming known that the endowment which made these animals so long an object of inquisitive wonder does not belong to them alone, but appears to be a special application of a common property, such as is frequent in the animal world. Since we have known that all nerves and muscles of all animals are capable of electrical actions, electrical fishes have indeed lost somewhat of their wonder, but this loss is abundantly compensated by the hope which now attaches to their investigation, that the solution of the great problems of the general physics of nerve and muscle may be promoted by it.

Until lately we had reason to regret, that of the three electrical

[1] My researches on electrical fishes are found in the following: I. Nachricht von einem nach Berlin erlangten lebenden Zitterwelse. Monatsberichte, etc., 1857, pp. 424–429; Moleschott's Untersuchungen zur Naturlehre des Menschens und der Thiere, 1858, vol. iv. p. 97. II. Ueber lebend nach Berlin gelangte Zitterwelse aus Westafrika. (Lecture given in the Friedrichsitze of the Academy on Jan. 28, 1858; containing a popular account of what had been ascertained up to that date about the Malapterurus). Monatsberichte, etc., 1858, pp. 84–111: Moleschott's Untersuchungen, etc., 1858, vol. v. p. 109. III. Bemerkungen über Reaction des elektrischen Organes und der Muskeln, Archiv für Anatomie, u. s. w. 1859, pp. 846–848. IV. Ueber Jodkalium Elektrolyse und Polarisation durch den Schlag des Zitterwelses. Monatsberichte, etc., 1861, pp. 1105–1128; Moleschott's Untersuchungen, etc., 1862, vol. viii. p. 549. V. Beschreibung einiger Vorrichtungen und Versuchsweisen zu elektro-physiologischen Zwecken. Abhandlungen der Akademie, 1862, Berlin, 1863, 4°. Physikalische Klasse. In §§ xviii and xix of this paper, pp. 148–162, the Frog-alarum and Frog-interrupter, of which I made use in the experiments on the Malapterurus, are described. VI. Ueber die räumliche Ausbreitung des Schlages der Zitterfische. Monatsberichte, etc., 1864, pp. 317–354; Moleschott's Untersuchungen, etc., 1865, vol. ix. p. 437. VII. Experimentalkritik der Entladungshypothese über die Wirkung von Nerv auf Muskel. Monatsberichte, etc., 1874, pp. 519–560. No. V is printed in the first volume of the Collected Papers, pp. 213–227. IV, VI, and VII follow here as Abh. XXIX, XXX, and XXXI. The present paper, XXVIII, takes the place of the three first numbers for the reasons stated in the preface to this volume.

fishes, one of them had remained as good as unknown to us. The electrical ray of European coasts[1] had been many times investigated since the revival of science in the seventeenth century, in all its relations, and each time with more perfect resources. The electrical eel had been investigated in its own home by Alexander von Humboldt, and this fish had already been brought often to Europe, and had been observed by the first experimenter of all times, by Faraday himself. On the other hand, the electrical sheath fish, or *Malapterurus electricus*[2], which inhabits the rivers of Africa, which was known to the ancients, and which is still no rare appearance in Bulák, the fish-market of Cairo, and which thus, next to the electrical ray, seemed the most accessible to science, was notwithstanding very little known. Until the year 1857 we possessed only isolated anatomical details which left even the coarse anatomy of its organ unexplained. As to its electrical action, there existed indeed already a valuable experiment on it, as will be shown hereafter, but this was so concealed in literature, that it might escape even the most earnest student of the subject. (See note to p. 388.)

A fortunate chain of circumstances has in so far supplied this want, that now the Malapterurus ranks with the Torpedo as one of the two electrical fishes of which the anatomy is best known; and that not only the most pressing physiological questions relating to it are answered, but light has been thrown on entirely new aspects of the phenomenon.

Theodor Bilharz, professor of anatomy in the medical school in Cairo, who has since unfortunately been snatched away from science by death, published in 1857 an anatomical description of the Malapterurus, worked out with the aid of modern appliances[3]. In this investigation he first obtained an insight into the structure of an electrical organ. Setting aside the parts intended for support and nourishment, such an organ, according to Bilharz, is to be regarded as a direct continuation of the nervous system. In an electrical organ a great number of small plates are arranged above

[1] For the sake of brevity, I speak of the family of the Torpediniae, so rich in genera and species, and which was increased by Linnaes' species *Raja Torpedo*, by the name of one of the three electrical fishes, i. e. Torpedo.

[2] Herr W. Peters has brought into use the name *Malopterurus*, which is at least somewhat more correct than the name framed by Lacépède, *Malapterurus* (instead of *Malakopterurus*). [Considering that Malapterurus is familiar to zoological students, it has been thought best to adopt that mode of spelling. Ed.]

[3] Das elektrische Organ des Zitterwelses anatomisch beschrieben, etc. Leipzig, 1857, Fol.

and by the side of each other, the substance of which, according to Bilharz, does not distinctly differ from the substance of ganglion cells. These are connected with the electrical nerves, and are the seat of the development of electricity; i. e. at the command of the electrical nerves the surfaces of all the little plates which look in one direction become positively electrical, and the opposite surfaces become negatively so. On this account the little plates are called electrical plates. The direction of the shock is always vertical to the plane of the plates. In the Torpedo, as the plates lie horizontally in the natural position of the fish, the direction of the shock is vertical in the organ from the belly to the back. In the Gymnotus, where the plates lie vertically, the direction of the shock is horizontal in the organ from the tail to the head. In the Malapterurus, according to Bilharz, the plates also lie in vertical planes. Thus we might infer that in this fish, as in the Gymnotus, the electricity will flow horizontally. But what will be the direction of the shock? Will positive electricity flow from the tail towards the head, in other words, will the front surface of the plates be the positive, and the back be the negative, as in the Gymnotus, or conversely?

On this point also Bilharz' investigations already permitted a conjecture. The connexion of the electrical plates with the nervous system is as follows. The electrical nerves, by continuous division, resolve themselves into numberless terminal branches, which finally sink into one of the surfaces of each electrical plate and are merged into its substance. As Signor Pacini has already observed [1], this embedding of the ends of the nerves in the case of the Torpedo and of the Gymnotus, is exclusively into that surface of the electrical plates which becomes negative in the discharge. Thus in the Torpedo this is the lower, and in the Gymnotus the posterior surface of the plate. Now in the Malapterurus, the nerves also seem to enter the posterior surface of the plates. Hence Bilharz inferred that in this fish, as in the Gymnotus at the moment of discharge, the posterior surface becomes negative, the anterior positive, that is, that the discharge in the organ would pass from back to front [2]. He was obliged to let the matter rest there, without being able to put this conclusion to the test of experiment. According to his account and that of Herr Mar-

[1] Sulla Struttura dell' Organo elettrico del Gimnoto e di altri pesci elettrici. Florence, 1852, p. 25.

[2] *Loc. cit.* p. 44.

kusen[1], the procuring of living Malapterurus in Cairo is attended with extraordinary difficulties, which are caused by the restrictions to which the sale of fish in Bulak is subject in consequence of taxation.

Thus the investigation came to a standstill in Egypt at the moment when it acquired the greatest interest, by the discovery of a connexion between the arrangement of the nerves and the direction of the discharge in the electrical organ, having been brought within view. But unexpectedly, the way was made plain for its prosecution from another quarter.

2. Living Malapterurus at Berlin. How they may be kept.

As early as 1855, Scotch missionaries sent some specimens of the Malapterurus in spirits to Edinburgh from Creek Town, a settlement situated about 90 kil. up the Old Calabar River. Mr. Andrew Murray thought that he recognised in them a new kind, which he named[2] *Malapterurus Beninensis*, after the Bay of Benin into which the Old Calabar river empties itself. In the summer of 1857, Mrs. Anderson, the wife of one of the missionaries, undertook to bring three living Malapterurus from Creek Town to Edinburgh, and carried out her project successfully in spite of shipwreck suffered on the way. In Edinburgh the fish came into Prof. Goodsir's hands, who was on the point of travelling to Berlin. He was so very obliging as to bring one of them with him, and as he saw that I was ready to devote myself to the subject, he had the other two sent subsequently.

This took place in August 1857. On a former occasion I described the arrangements which I made, in order to preserve the fish in life and health. It would be useless to repeat this description, as the same difficulties will not occur again. Besides, at first, my exertions were not very successful. Only one of the three fish lived until January of the following year. I will, however, give the method which I finally adopted for the preservation of malapterurus, as they may possibly be useful.

In the summer of 1858, I received three from Goodsir and my friend Dr. Bence Jones of London[3], but one of them died very

[1] Bulletin physico-mathématique de l'Académie de St. Pétersburg, t. xii. 1854, p. 203.

[2] The Edinburgh New Philosophical Journal, New Series, 1855, vol. ii. pp. 49, 379; vol. iii. p. 188; Report of the British Association, etc., 1855. Transactions of the Sections, p. 114.

[3] They belonged indeed to the same consignment. Bence Jones sent two from

soon. In the summer of 1859, Bence Jones sent two fish through the captain of a ship by way of Liverpool. The ship, which brought them from Hull to Hamburg, had such a stormy passage, that on arrival here, one fish was dead, and the other apparently dying, with white corneas and bent barbels. I succeeded in restoring it, by exposing it for weeks to a stream of fresh water, and it was just this fish which lived longest of all, till the autumn of 1864, and it grew considerably in confinement.

I kept the Malapterurus in a trough four feet (125 cm.) long, one foot and a half (47 cm.) broad, and two feet (63 cm.) deep, the floor of which was formed by a slab of slate, and its walls were of plate glass. The trough was filled with tap-water up to 5 cm. from the edge, which was renewed at a sufficient rate. In order to maintain the temperature at the proper height, the trough stood in a zinc case five feet (157 cm.) long, two feet (63 cm.) broad, and thirteen inches (34 cm.) deep, encased in wood with a layer of saw-dust, and its lid was fitted closely to the glass plates by means of a packing of tow. The water in the zinc case was warmed by a small copper boiler arranged at the side, the source of heat being an Argand gas burner, so that a thermometer floating in the trough indicated 17·5—20°C. Goodsir had told me that 70° Fah. = 21·1°C is the proper temperature for the fish. But I found accidentally, that they bore a temperature of only 15°, and at one time, when I fed the trough with spring-water, the Malapterurus which was then the sole inhabitant of it, always sought out the very spot at which water at only about 11° was flowing in. As the animal was in a state of inanition, perhaps its instinct impelled it to diminish its respiration and thereby its need of nourishment; for Liebig's assertion: 'It is not a difficult task to endure hunger for a long time at the Equator, but cold and hunger wear away the body in a short time'[1]—does not hold good for animals of variable temperature.

Malapterurus take refuge in the dark whenever they can. I covered the trough therefore with a wooden black varnished lid, which shut out the light almost entirely, but admitted air. Water plants in the trough and earth at the bottom of it make cleanliness more difficult, without proving to be of any use. The trough must

London by way of Hamburg, and Dr. Turner, at that time Goodsir's demonstrator of Anatomy, had the goodness to bring the third with him by way of Leith and Hamburg.

[1] Chemische Briefe, 3rd Edn. Heidelberg, 1851, p. 401.

be divided by a fine trellis of varnished iron wire, into as many divisions as there are Malapterurus to be kept, for these animals carry on violent battles, in which they chase each other, bite one another and will not let go their hold, and thus naturally wear themselves out. They also attack other fish furiously and kill them with electric shocks (see the following section). Whether they discharge electric shocks in their battles with each other, I do not know.

It fortunately proved very easy to feed the fish. As, in the specimen in spirits of wine which reached Edinburgh, the intestine contained remains of fresh water crustacea, an effort was made both there and here to procure similar kinds (*gammarus, asellus, daphnia*, etc.) for them. But as this was difficult, earthworms were tried in Edinburgh as food, and as this was successful, worms were given to the fish here also, so long as there were any to be had, in the autumn. One of them took the worms out of the pincers, swallowed them down without giving them a shock, with a quick sucking motion, and rose to the surface as if asking for more, so that one might consider it as, to a certain extent, tame. When later in the year we fell short of worms, the idea occurred to Graff, the keeper, to give the fish strips of beef like worms, and they not only devoured them eagerly, but this food also evidently agreed with them very well; perhaps even better than worms, which generally swarm with parasites, and which therefore were discontinued also in summer for later consignments of fish.

Exact information is wanting as to how the Malapterurus accomplished the journey from Africa to Scotland. They were brought here from Scotland or England, each one singly with some water-plants in a gold-fish bowl with a cover of basket-work, which fitted so exactly that the cover seemed as if plaited over the bowl. It was hung up by the handle of the cover in the cabin or the railway carriage. The water-plants answered the purpose of lessening the shaking of the water and protecting the fish from knocks.

3. Natural History. Habits of the Malapterurus.

With the aid of the rich material of the Berlin collections, Herr Peters, who had observed the living Malapterurus in South-east Africa, answered in the negative the question, whether that from

[1] Monatsberichte, etc., 1868, p. 121; Naturwissenschaftliche Reise nach Mozambique, etc., Zoologie IV, Flussfische. Berlin, 1868, 4°. p. 41.

West Africa is a new species. I refer to his[1] paper for the zoological characteristics, which at first sight and with less complete comparison, had led to this suggestion.

Our specimens were all small, without barbels, between 12·5 and 27·5 cm. long, whilst Bilharz measured one of 22″=57·5 cm. The quick growth of one which was kept alive longest, seems to show that the creatures were still young. Most of them were females.

It is impossible to form a good idea of Malapterurus from specimens in spirits of wine and from drawings taken from them. In drawings, the position in which the barbels are held is particularly incorrect, as they are represented as hanging down in a flabby manner and curled, whilst in the healthy fish they are extended in straight lines and far apart (see Figs. 10, 11).

Another characteristic in the appearance of the Malapterurus, which is no longer recognisable in specimens in spirits of wine, consists of beautiful, regular, broad transverse folds, which in our fish were always 5–8 mm. in size (unquestionably more in larger fish), and which show themselves on the concave side of the fish when it bends laterally. They are made by the organ which envelops the fish in the form of a thick walled tube, the outer layers of which arrange themselves in folds over the contracted muscles of the flanks, whereas in other fish, the thin and firmly attached skin always follows exactly the contour of the body.

In life, the organ as well as the skin covering it, is transparent, so that in the light one looks into its reddish depth. In death, especially in specimens in spirits, it is dim and opaque. The general colour of such specimens is gray; in life, our fish were brown except the black spots with which they were, as it were, sprinkled on the back; the weaker ones were yellowish brown, the stronger ones were rather deep red brown. The colour even of the same fish varied. In the dark they became blackish, under the effect of light, bright again. When fatigued by experiments they looked pale, after resting for a few days they appeared again deeper coloured.

The animals usually remained motionless in the darkest part of the bottom of the tank with barbels far extended. At night they seem to become more lively; at least in Creek Town, fishes which were kept in readiness to be shipped off, perished through jumping out of their vessels during the night. When the fish had fresh water given to them in the tubs in which I originally kept

them[1], they swam about briskly in the little whirlpool, and as the 'frog-alarum' showed (see below, p. 384), discharged their batteries repeatedly, whether to ward off fancied danger, or as an expression of content, it would be difficult to say. One of the fish had evidently taken a dislike to the electrodes of the frog-alarum, and often attacked it with bites, which it accompanied with several discharges following rapidly on each other. The sight of red colours, e. g. of a stick of sealing-wax, did not appear to excite the Malapterurus in the same way as it does frogs and some other animals.

Generally the Malapterurus answer every touch, even by a non-conductor, with one or more discharges. Sometimes, however, they escape from the hand by a violent movement, without giving a shock. This shows that in the former case the discharges are voluntary and not merely reflex. The frog-alarum also showed (see below, p. 384) that the fish discharged many times without any assignable cause.

Other fish, which are put into the water with the Malapterurus, are immediately attacked by them with electrical broadsides. One sees the fish immediately lose their balance and drift apparently lifeless with the side towards the light. If they are withdrawn at once, such fish come to themselves again. Given over to their fate, they die. The three first Malapterurus which reached Edinburgh, killed all the gold-fish in the tank of a hot-house.

One afternoon (in September, 1857) I placed in each of the tubs just mentioned, with the Malapterurus already in it, a tench (*tinca chrysitis*) about 15 c.m. long, and a loach (*cobitis fossilis*) of the same length. A violent tumult at once arose in the three tubs. Here and there a tench leapt into the air, whilst the loaches, twisting themselves in an eel-like fashion, coursed round the circumference of the surface of water as if driven by deadly fear, and at last, one after the other, threw themselves over the edge of the tub, 2·5 cm. high, between the tub and the wire netting covering it. When they were put in again, they escaped repeatedly, until I made the edge twice as high, by letting off the water. Naturally, each electrical fish of prey had equally distressed both tench and loach, and the water had become turbid in each case, by the stirring up of the earth with which at that time I still kept the bottom of the tubs covered (see above p. 373). I should have remained in the

[1] They were of the same kind as those described in the following paragraphs as experimental tubs.

dark as to the precise course of events, if I had not taken the precaution to place the electrodes of the frog-alarum in one of the tubs. But this betrayed clearly enough what took place. Its bell went on ringing continuously, indicating now a strong, now a weak branch current in the nerve, either because the fish discharged with different strength, or because the electrodes took up a more favourable position at the moment of the discharge. The hammer seemed sometimes to stick to the bell, indicating that the electrical fish was tetanising its victim. Now followed an interval of peace, until presumably, the tench, aroused from their stupefaction, began again to move, and the Malapterurus also rested, felt disposed for a fresh attack. Ever and anon the tumult started again, now in one vessel, now in the other; the individual periods, however, became always shorter, and were separated by longer intervals. I then left the field of battle. When I came into the laboratory the next morning, the loaches lay dead upon the ground. Thus during the night, they had again escaped even over the edge of the tubs 5 cm. high. In the tubs of the two larger fish, the tench were dead. They must have been dead a long time, because they were stiff and their corneas had begun to cloud. The water was clear, thus peace had long prevailed. The little adventure did not seem to have affected the Malapterurus. The smallest had not been able to kill its tench, but it died very shortly after, although I put it in another vessel. A fourth couple of tench and loach, which I kept as a check on the experiments in a fourth tub, under circumstances quite the same in other respects, lived for weeks afterwards.

A frog, under the effect of the discharge of the Malapterurus, stretches itself as in tetanus from strychnine. But on account of the poisonous skin secretion of the batrachians[1], I did not make any experiment with them, similar to the foregoing one. The fish allowed earth-worms to curl themselves about their barbels without discharging (comp. above, p. 374). But in general they seemed not to give a shock when their barbels were touched, but to draw back; on the other hand, as already observed, when the skin was touched, they discharged almost invariably.

When the fish became ill, they changed their habits very much. They forgot their fear of light, and without allowing themselves to be frightened away by the proximity of an observer, they kept themselves at the surface by a quick and laboured action of their

[1] Untersuchungen, etc., vol. ii. Abth. i. p. 17. Anm. 2. Comp. Gratiolet et Cloëz, Comptes rendus, etc., 1851; t. xxxii. p. 592.

pectoral fins, and by supporting the tail on near objects. At the same time they breathed extremely fast, half water, half air, with the upper jaw out of the water. They expelled the water mostly from the mouth, more rarely from the gills, so that at each breath they threw up bubbles, and soon a wreath of foam of large bubbles surrounded them. Many fish, among others the Gymnotus[1], rise to the surface to take in air, but this throwing up of bubbles was recognised by our keeper Graff as a sign of distress and weakness in fishes. Malapterurus in this condition no longer discharged on being touched; the barbels were no longer stretched out in straight lines, the skin became wrinkled and ulcerated; blood issued from the fins and the gill-covers; sometimes at last a violent motion convulsed the jaws and gills. Fish so affected inevitably died. Aeration of the water by means of bellows remained without result. Such fish ought to be used systematically in good time for experiments, instead of delaying, as I unfortunately often did, until they were found dead, in which case it is not only impossible to experiment, but the event may be observed so late, that the fish are useless even for histological purposes. One can, however, be never quite secure against this mishap, for the fish may die without clear premonitory symptoms, and as they generally lie quiet deep down, their death may remain unnoticed so long, that nothing more can be done with them.

4. Mode of experimenting with living Malapterurus.

After the above experience there is no doubt that of the three electrical fishes, the Malapterurus is the best fitted to be kept in confinement. The Torpedo, as an inhabitant of the sea, cannot bear comparison with it[2]; the Gymnotus, while it can be kept equally

[1] Comp. Edw. Bancroft, An Essay on the Natural History of Guiana, London, 1879, p. 192.

Hugh Williamson, Philosophical Transactions, etc., 1775, p. 94; Alex. Garden, ibidem, p. 102; Humboldt, Recueil d'Observations de Zoologie et d'Anatomie comparée, etc., Paris, 1811, 4°. p. 61; Faraday, Experimental Researches in Electricity. Reprinted from the Philosophical Transactions, etc., vol. ii. London, 1844, p. 3. Ser. XV. § 1753. (The paper, frequently quoted in the following, by Faraday, upon the electric eel, is also found in Poggendorff's Annalen, etc., 1842, Ergänzungsband, p. 391.)

[2] Until the formation of zoological stations, no one in my knowledge has succeeded in keeping the Torpedo alive longer than fifteen days, and John Dary is the only one who was so fortunate. (Researches physiological and anatomical, London, 1839, vol. i. p. 48; comp. Faraday, Experimental Researches, etc., *loc. cit.* p. 2, § 1752.) John Todd, who made his observations at the Cape of Good Hope, and therefore presumably on *Astrape Capensis* Müll. Henl., (Philosophical Transactions, etc., 1816,

long, is inconvenient on account of its size and the force of its discharges.

But of the three electrical fishes, it is again the Malapterurus, which is the best suited for all experiments in which the electrical nerves have to be dealt with; as, for example, when these have to be employed in connexion with the organ, in the same way as a muscle nerve is used in connexion with the muscle. In the Malapterurus, each lateral half of the organ is provided with a single nerve, which one cut exposes to a considerable length almost without bleeding. The electrical nerve is, as it were, already prepared by nature; indeed the same cut suffices for both nerves. In the Torpedo, each organ contains four, comparatively much shorter nerves, which demand far more skilful preparation and greater injury in order to expose them, than the one nerve in the Malapterurus. Moreover, in the Gymnotus, each half of the chief and accessory organ is provided with over two hundred nerves, all of which it is impossible to prepare and deal with experimentally at the same time in the living animal. I do not speak of the unusual interest which the investigation of the electrical nerve of the Malapterurus offers on account of its structure, hitherto unique in the animal world, and of its origin from a giant ganglion cell[1]. Add to this, that the tissues of the Malapterurus, inclusive of the electrical organ, appeared to me to possess great tenacity of life, recalling that of the frog. But in order to make the most of these advantages, one must have at command any required number of animals, and this would be possible only in their own home. With two or three fishes, whose life must be spared because much still remains to be ascertained about the living animal, one cannot set on foot researches in which one needs a fresh preparation for almost each experiment, as in the investigation of nerve and muscle. Imagine what it would be in the investigation of nerve and muscle, to be limited to the use of two or three uninjured living frogs. Such a consideration may serve to undeceive

p. 120), and Saint-Linari (Bibliothèque universelle de Genève, Avril, 1837, vol. viii. p. 395) kept them alive only five days, Matteucci only three days (Essai sur les Phénomènes électriques des Animaux. Paris, 1840, p. 52.)

[1] One might suspect, that in the Gymnotus also, the electrical nerves are the Deiters' processes of as many giant ganglion cells. M. Schultze, however, saw in the electrical nerves, ordinary nerve tubes, and in the anterior half of the spinal-cord, a remarkable number of large ganglion cells (Zur Kenntniss der elektrischen Organe der Fische. Specially reprinted from the 4th vol. of Abhandlungen der Naturforschenden Gesellschaft in Halle, 1858, pp. 30, 32, 33). This leads us rather to infer the existence of a structure similar to that of the Lobus electricus in the brain of the Torpedo (comp. M. Reichenheim in the Archiv für Anatomie, etc., 1873, p. 751).

those who form an exaggerated idea of what can be determined with a few live Malapterurus in the laboratory, and to whom my results may seem too meagre.

Add to this, that the methods of investigation had to be almost entirely contrived. I will relate first, how I was provided in this respect.

1. *Observation of the shock of the Malapterurus with reflecting magnet, scale, and telescope.*

By the term experimental circuit, will henceforth be understood the system of conduction by which the discharge of the fish is led off, in order to examine any of its effects, whether the circuit be interrupted or not. A Wiedemann's galvanometer was usually introduced into it in order to measure the discharge.

In all earlier experiments with Malapterurus, ordinary multipliers with astatic pairs of needles had been used. Apart from the fact that they are ill-fitted for measurements, such an instrument is here especially unserviceable. At times I found that the needles are caught by the shock when they are at a great angle to the direction of the coil, by which they are either rendered no longer astatic, or may be even almost entirely demagnetised or reversed. Observation of the deflections with mirror, scale, and telescope could never be more advantageously made than here, and Herr Eckhard and I introduced them simultaneously, he at Trieste in experiments on the Torpedo, and I here in those on the Malapterurus. When a Wiedemann's galvanometer was used, and one of the thermo-bobbins containing 53 turns of wire was allowed to act at a distance of 25–75 mm. on a heavy reflecting magnet not rendered astatic, I obtained measured deflections from the discharge of the Malapterurus, without risk of a disturbing effect on its magnetism. The aperiodic magnet would have been of great advantage in these observations, but at that time I had not got so far.

2. *The leading-off cover.*

The shock of the fish in the experimental circuit is weakened by derivation, in proportion as the mass of water in which the fish is contained is greater. The action of the fish is also physiologically violent as the quantity of water is less. Thus they were less able to kill other fish in the trough than in the tubs. That they were able to do so in the Edinburgh basins, which were certainly not

smaller than our troughs, must have depended on their greater strength at that time (see above, p. 376).

In their own home, where the supply of Malapterurus is unlimited, an observer would not scruple to take the fish out of the water, and thus get rid of the derivation due to immersion in water. When the fish is in the air, this derivation is confined to its body. But I could not venture to do this. I could only as far as possible diminish the water-derivation.

The fish to be observed was caught in the landing-net and removed to a shallow cylindrical tub, the experimental tub, filled with water. This was made of coarse porcelain (Gesundheitsgeschirr) having a diameter of 295 mm. and a depth of 125 mm. That the removal was not effected without violent shocks was proved in a way which will be stated later. For reasons which will also be stated later, an unsilvered glass plate having the same diameter as the tub was placed at the bottom of it. The water was drawn off by a siphon, until the surface just touched the back of the fish. The mass of water surrounding the fish was thus diminished as much as seemed compatible with its well-being during the experiment, and the discharge could be led off as advantageously as possible without raising the fish into the air[1].

In order to lead off the discharge, the means used by Faraday[2] for the Gymnotus first suggests itself; this is, to apply to the fish two metal saddles which are insulated excepting at the surface of contact. A telegraph wire, insulated by guttapercha, is soldered to the middle of the arch of the saddle, and serves both as a handle and for leading-off the current. The saddles are made of different shape and size, and of different metals[3] as occasion requires. Generally they are bands of platinum 5 cm. long, 1 cm. wide, bent to the contour of the fish at different parts of the body. But even the inequalities of zinc mostly vanish as compared with the shock; if they do not, they are compensated.

If it is desired to lead as large a proportion as possible of the shock into the experimental circuit, then the contrivance for leading-off must be somewhat different. Faraday, who needed to be even more careful with his Gymnotus than I with my Malapterurus,

[1] The late A. v. Bezold, who was helpful to me in many ways in these experiments, proposed to replace ordinary tap water by aerated distilled water, in order to intensify the discharge.

[2] Experimental Researches, etc., *loc. cit.* p. 5, § 1758.

[3] See the following paper, §§ 1, 3, 4.

endeavoured to diminish the derivation by the water, by insulating the fish from the water at the moment of the shock. But he attempted this with only the two parts of the fish within the saddle, whereas I proposed the same thing for the part also between the saddles. In this respect the Malapterurus offered great advantages over the long Gymnotus with its lateral movement.

Fig. 10 shows the contrivance with which I attained my object. It has been not inaptly compared to the cover of a mummy coffin. It consists of a guttapercha cover, which, when the fish rests on the glass plate at the bottom of the tub, fits as closely as possible to its body above and at the side, and touches the plate

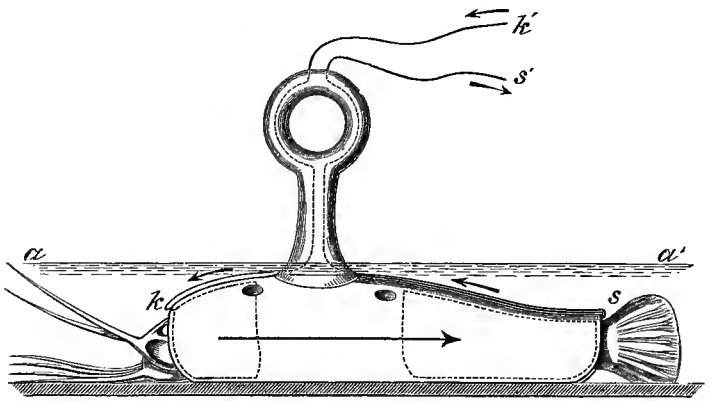

Fig. 10.

with its lower free edge. $a\,a'$ is the surface of the water in the tub; for the sake of clearness, it is shown higher than was usual (see above). In order to prepare such a cover for any particular fish, I cut out a model of the fish in lime wood. This served as a last over which the guttapercha, softened in hot water, could be moulded. When the guttapercha had hardened, it was cut off in a line with the lower edge of the last, the cut edge was again softened and flattened on a glass plate wetted with hot water. A handle of guttapercha is welded on to the back of the cover. Inside this cover, at the ends corresponding to the head and tail of the fish, are linings of tinfoil stuck on with shellac; these are indicated in the figure by dotted lines. At the ends *k* and *s* of the cover, these linings are connected with strips of tinfoil, which, protected by insulating material, pass along the back of the cover to the handle, where

they are soldered to the small copper plates in which the wires end. These wires, after an insulated course, come to view (k', s') at the upper end of the handle. The cover is open before and behind in order to leave the barbels and the tail free.

In using this contrivance, one waits for the moment when the fish is lying nearly across the experimental tub. The cover is then held horizontally over it, until it settles in the most favourable position, and is then quickly placed upon it. In order that the air between the tinfoil lining and the fish may escape, two holes are bored in the cover at its inner edge with a hot punch. Almost at the instant that the cover touches the fish, it gives a shock; but as it is insulated in every direction excepting where the head and tail are exposed, a considerable strengthening of the discharge is produced, as the following experiment teaches.

I prepared a cover, which differed from another intended for the same fish in this respect, that the guttapercha wall between the two lined ends was removed and was replaced by three glass rods. The results in divisions of the scale were as follows:—

	1	2	3	4	5	6	*Mean.*
With the partial cover.....	73		82		71		75·3
With the complete cover...		191		141		121	151·0

The insulation of the fish, by means of the cover, doubles therefore the strength of the shock in the experimental circuit. The covers would undoubtedly have worked still better, if they had also included the tail. That the covers often enclosed the fish before it discharged, is shown by the observation that when they were applied, the frog-alarum not unfrequently remained inactive from the insufficiency of the branch current in the excitation tube. If the fish discharges, as it generally does, several times after the excitation, the leading-off cover has also the advantage, that the following shocks are sure to be led through the experimental circuit, whereas the fish cannot be held firmly with the loose saddles, without hurting it.

Between every two experiments, the cover is put in another tub of water, in order that inequalities in the tinfoil linings may be removed. They are not put in the same tub, because the fish is thereby disturbed, and, probably taking the cover for another fish, discharges frequent electric shocks at it (see above, p. 376).

3. *Frog-alarum and frog-interrupter.*

One of the greatest improvements which I made in the method of these experiments, consisted in perfecting a contrivance which Galvani had already used in 1797 in his experiments on the Torpedo[1], namely, in employing a nerve muscle preparation of the frog, in order to make the twitches produced by the shock serve a double purpose.

First, the preparation indicates that the fish has discharged, as to which no certainty can otherwise be had, as the shock produces no visible effect in the fish itself, and the absence of any action in the experimental circuit may be dependent on defect in the circuit. Galvani and Matteucci were content with laying the frog preparations on the Torpedo itself and observing the twitches. I diverted a part of the discharge passing through the mass of water in the experimental tub, led it through the nerves which were in contact with the ring electrodes of the 'moist excitation tube,' and let the muscle indicate its contraction by ringing a bell. This was the origin of the 'frog-alarum[2],' which is described in detail, and of which a diagram is given in a former paper, and I will therefore not repeat it here. Within the limits of accuracy there stated, the frog-alarum affords a means of watching the electrical activity of a fish in the experimental tub for many hours together (comp. above, p. 377). If the electrodes of the excitation tube were connected by wires with the iron hoop of the landing-net and with a small iron disk at the bottom of the net, the frog-alarum indicated the discharges made by the fish during its removal from the trough to the experimental tub, but for the most part, these did not begin to act until the fish emerged from the large mass of water in the trough[3].

[1] Memorie sulla Elettricità animale . . . al celebre Abate Lazzaro Spallanzani, Bologna, 1797, 4°. p. 74; Opere edite ed inedite ec. Bologna, 1841, 4°. pp. 411, 412. Matteucci made use of the same contrivance without naming Galvani (Essai sur les phénomènes electro-physiologiques des Animaux, Paris, p. 144; Lezioni di Elettro-Fisiologia ec. Torino, 1856, p. 2; Corso di Elettro-Fisiologia ec. Torino, 1861, p. 115).

[2] See 'Description of some apparatus and modes of experiment,' etc., Gesammelte Abhl. vol. i. p. 213. [Fig. 11 with its description are interpolated from a previously published paper, not included in this volume. Ed.]

[3] Comp. above, p. 380.—Gay-Lussac had already observed the intensifying of the discharges in Torpedos, when they were lifted out of the water (Humboldt, Observations, etc., p. 79). The fact recalls the disappearance of the current of a gastrocnemius immersed in a dilute salt solution.

The second purpose for which the frog-preparation is adapted in experiments on electrical fishes is the following. The frog-alarum teaches that the excited Malapterurus, if it is at all vigorous, seldom discharges once only. Generally two or three strokes of the bell occur, sometimes following each other closely, sometimes separated by a longer interval. Without having recourse to other means, it is therefore impossible to ascertain the effect which any given condition exercises on the strength of the branch current led into the experimental circuit. For it always remains doubtful, whether the differences observable result from that condition, or from the varying number and succession of the discharges. For reasons easily understood, nothing could be effected here with the usual mechanical means. But it is obvious that the frog-preparation might be relied on for the timely opening of the experimental circuit after excitation by the first shock. With a given nerve-length and a muscle of given size and efficiency, the muscle raises

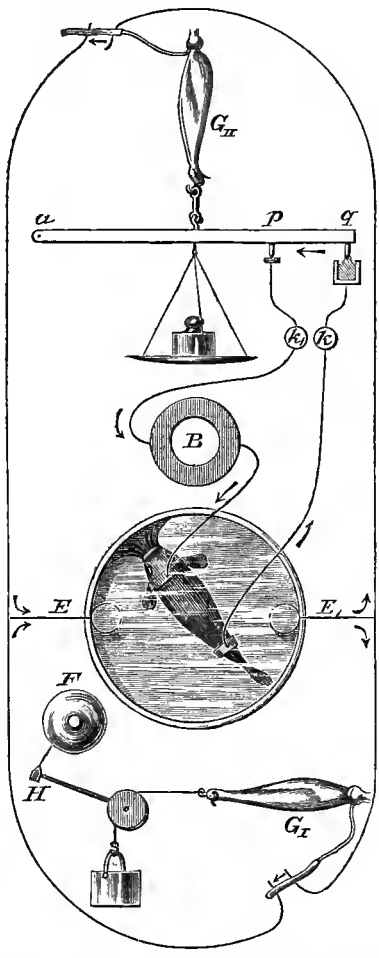

Fig. 11. E and E_1, zinc electrodes in the trough containing the fish. F, H, G_I, the bell, hammer, and muscle arranged to form an alarum. a, p, q, lever of the frog-interrupter. G_{II}, its muscle. p, the platinum point which rests upon the supporting plate. q, amalgamated copper wire which dips into mercury. K, K_1, keys. B, galvanometer. The action of the interrupter is such, that only one shock can pass through the galvanometer, for by the contraction of the muscle G_I, the galvanometer circuit is broken at q and not again closed. The alarum of course goes on ringing.

a given overweight in an interval which, after an inappreciably short excitation of the nerve, is always the same, and this action could be employed to open the experimental circuit. The only question was, how the time relations of the twitch corresponded to those of the shock, about which nothing was then known[1]. The first experiments taught me that the duration of the shock is of the same order with the duration of the twitch, and this led to the construction of the 'frog-interrupter,' which has also been already described in detail and accurately drawn, and its properties tested[2]. I need not therefore dwell upon it here. As was there stated, it is a more convenient form of the same contrivance used by Helmholtz in measuring the velocity of excitation in the nerve after Pouillet's method, and in accordance with this more general character it has acquired importance[3] in many relations. In the present experiments it serves the following purposes: 1. it allows only the first of the several shocks which the fish successively makes to pass into the experimental circuit; 2. it admits a proportion of the first shock, which is greater or less according to the overweight used, and which, provided that the shocks have similar course but different strengths, is also proportional to the strength; 3. it may be used to break a derivation circuit by which the shock had previously been kept out of the experimental circuit. We shall investigate later (in § 10) with what degree of certainty the frog-interrupter executes the second task. As, in general, it affords entrance for a part only of the shock into the experimental circuit, it is evident that when it is used, greater sensitiveness of the galvanometer is requisite.

Each fish was always worked with, only after intervals of several days. I usually put the saddles or covers on it every ten minutes, and I went on for an hour and a half or two hours[4]. Including the

[1] Herr Eckhard showed at the same time in Trieste with Torpedos, that the shock must last longer than an opening induction shock. (Beiträge zur Anatomie und Physiologie, vol. i. Giessen, 1858. 4°. p. 168, 169 ff). Since then, Herr Marey, in Naples, has investigated the duration of the shock in Torpedos, with the Pendulum-myograph, and found it to be 1/14″, which confirms my result (Comptes rendus, etc., 1871, vol. lxxiii. p. 918). I do not need to remark, that myograph experiments on living uninjured fish would meet with almost insuperable difficulties, so that I had to forego them.

[2] Gesammelte Abhandl., vol. i. p. 215 ff. Pl. III. Fig. 12. 12a. Comp. the following paper, § 3, Fig. 44.

[3] *Loc. cit.* vol. i. p. 227, note, where several applications of the frog-interrupter are mentioned; Holmgren's investigation of the course of the gastrocnemius variation carried out with its help, is not alluded to.

[4] Gesammelte Abhandl., vol. i. p. 221.

removal of the fish from the trough to the experimental tub and back again, it was excited eleven to fourteen times; however, it gave at least twice or thrice as many shocks. In the course of such a series of experiments, the fish became evidently fatigued. It became pale (see above, p. 375), and at last responded with one discharge only when the cover was put on. In certain respects this was advantageous; it could not, however, be depended on, as the fish not unfrequently grew impatient towards the end of the series, and unexpectedly gave several exceedingly strong shocks following each other rapidly.

One difficulty of experiments with Malapterurus in the form which I gave to them, lies in the necessity for three observers—one to manipulate the fish, one to sit at the telescope, and one to watch the frog-interrupter. I take this opportunity to express my tardy, but not less hearty thanks to Messrs. Pflüger, G. Quincke, and Rosenthal, who gave me their assistance at that time.

5. Subjective testing of the shock of the Malapterurus.

In comparison with its size, the shock of Malapterurus is surprisingly violent. If the head and tail of a powerful fish are touched with the fore-fingers in the water, the shock does not extend beyond the knuckles. If it is seized with hands thoroughly wetted, a severe shock is received up to the elbow. If it is touched with one hand, a pricking sensation is experienced in the skin, a burning one in wounds, and a painful shock is felt in all the joints of the submerged parts. The best way to take the shock is to hold with wet hands, ordinary metal handles which are connected by long wires with the linings of a leading-off cover, and to let an assistant put this on the fish. As one is accustomed to test electric shocks in this way, and is not disturbed by anxiety to get proper hold of the fish without hurting it, or by the feeling of repulsion at laying hold of it, one can better judge of the sensation caused by the shock. The shock does not seem so sharp as that of a Leyden jar, but has a somewhat swelling character. Several maxima may be frequently distinguished in it. By sending opening shocks of an induction apparatus, with two Groves in the primary circuit, through the water of an experimental tub, by means of copper plates plunged into it, having first approximated the secondary coil to the primary as closely as possible, the shock which I experienced when my hands were immersed in the water, was certainly

not stronger than that of a vigorous fish[1]. An opening shock with the coil quite pushed in and one Grove in the circuit, taken directly through the handles, has about the same strength as such a shock.

6. Of the direction of the shock in the Malapterurus.

The simplest observation teaches that, in accordance with Bilharz' prediction, the motion of electricity in the organ of the Malapterurus occurs in the direction of its length. But the further surmise, inferred by Bilharz from Pacini's rule, that the current in the organ of this fish would flow from the tail to the head, as in that of the Gymnotus (see above, p. 371), has not been confirmed.

The very first experiment which I made on the 13th August, 1857, with the fish brought with him by Prof. Goodsir, and which I communicated[2] to the Academy on the same day, was the reverse of what Bilharz had inferred from the microscopical appearances, with what seemed to be such complete justification. It has since then been established in numerous experiments, that the shock in the organ of the Malapterurus is invariably directed from the head towards the tail. Just as a column of the organ of Torpedo would have to bend forwards with its upper end in order to become a column of the organ of Gymnotus, so it would have to bend backwards with the same end in order to become one of the organ of Malapterurus.

The hope of finding a constant relation between the nerve-ending and the distribution of tension in the electrical plates seemed thus shut out. But a remarkable way out of this difficulty presented itself. Ecker had observed shortly before in the pseudo-electrical organs of certain species of Mormyrus (*M. dorsalis* and *anguilloides*), that the nerve-tubes do not pass directly into the surfaces of the pseudo-electrical plates turned towards them, but go into the plates as though through sharply punched holes; they then swell knob-like,

[1] Comp. a corresponding experiment on the Gymnotus, Ges. Abh. xxx. § 4.

[2] Monatsberichte, etc., 1857, p. 424. As early as 1855, the Florentine surgeon, Ranzi, who died shortly afterwards, and who had resided in Egypt for the sake of his health, had determined the direction of the discharge of the Malapterurus by irreproachable experiments, using silver spoons as electrodes. I was unacquainted with these experiments, because they were only printed in the two first volumes of the *Nuovo Cimento*, which were not to be had either in Berlin or Göttingen until much later, so that I was obliged to obtain a copy of the essay from Italy (Comp. Archiv für Anatomie, etc., 1859, p. 209).

and finally send [1] numerous ramifications backwards into the surfaces originally turned away from their direction of distribution. Max Schultze (then in Halle) recognised in Bilharz' drawings of the electrical plates of the Malapterurus, traces of a similar arrangement, and the thought struck him, that this might be the explanation of the discrepancy between Bilharz' result and that observed by me. After I had sent to Schultze pieces of the organ of the Malapterurus —some as fresh as possible, some preserved in suitable liquids—he succeeded, as he believed, in confirming with certainty his previous conjecture.

According to him, the nerve-tubes enter the posterior positive surface of the electrical plates indeed, but do not sink into them. They go through a hole in the middle of the plate to its anterior negative side, and there spread out backwards in the shape of a bell. The edge of the bell, as corresponding with the true nerve-ending, blends with the negative surface of the plate at the circumference of the hole [2]. Thus Pacini's rule might still hold good, according to which, that surface of an electrical plate into which the nerves bury themselves is always negative at the moment of the shock; but in the case of Malapterurus and of those species of Mormyrus, in virtue of the peculiar arrangement described, the surface which, according to this rule, ought to be negative, becomes positive, and conversely.

Schultze's successors reject this explanation. The character of the membrane scarcely admits of its being considered as an expansion of the nerve, itself flat, which spreads into it, and it must be admitted that it is as often seen to continue into the plate in a transverse plane, as to originate in the form of a bell [3] with its edge to the anterior circumference of the hole.

Another reason, hitherto disregarded, in opposition to Pacini's rule, has its weight. Robin succeeded apparently, where Joh. Müller and Matteucci failed, in eliciting a shock from the pseudo-electrical organ of the common skate [4]. In this organ the nerves terminate at the

[1] Untersuchungen zur Ichthyologie, etc. Freiburg, vol. i. 1857, 4°. p. 29.

[2] Zur Kenntniss der elektrischen Organe, etc., *loc. cit.* pp. 14, 15.

[3] Comp. R. Hartmann in the Archiv für Anatomie, etc., 1861, p. 661. F. Boll in Schultze's Archiv für mikroscopische Anatomie, 1873, vol. x. p. 242. Babuchin in Centralblatt für die medicinischen Wissenschaften, 1875, pp. 131, 132.

[4] See my Berichte in den Fortschritten der Physik im Jahre, 1846, etc. II. Jahrgang. Berlin, 1848, p. 469; in the year 1847, III. Jahrgang. 1850, p. 440; comp. Untersuchungen, etc., vol. ii. part i. p. 207; Peters never obtained a shock from the Mormyri. The natives were also unaware of any striking property of these fish. But he only came across emaciated fish, the electrical organs of which

anterior side of the plates. The direction of the shock ought therefore to be, as Max Schultze already supposed, the same as that in Malapterurus [1]. According to Robin, it would be the opposite [2]. He did not himself perceive the bearing of his statement; this is not to be wondered at, as he did not even know that the direction of the shock is different in the Gymnotus and Malapterurus [3].

7. Physical Investigation of the shock of the Malapterurus.

The discovery of the Leyden jar, towards the middle of last century, quickly put an end to the theories of the older physicists as to the shock of electrical fish, and its explanation by stupefying emanations or mechanical shock. After Adanson on the Senegal, in 1751, had observed the similarity of the discharge of the Leyden jar and of the sensation produced by the Malapterurus [4], the endeavour arose to prove the identity of the cause of both phenomena in other ways. The attempt was made to reproduce by means of the shock of electrical fish other electrical actions, and particularly to show that the conductors and non-conductors of both are the same. In spite of the efforts of Walsh [5], Cavendish [6], Configliachi [7] and others, there still remained sufficient uncertainty in regard to this point to induce Humphry Davy [8] to express shortly before his death, the opinion that the electricity of electrical fishes might be different from ordinary electricity. Faraday, indeed, only four years later,

had wasted away to the tendinous sheath. Unfortunately, he could not ascertain if this arose from individual differences, or if it was a question of periodical conditions dependent on the season of the year and spawning time (Naturwissenschaftliche Reise nach Mossambique, etc., *loc. cit.* p. 33). For further testimony as to the inactivity of the organs of Mormyrus, see Hartmann, in the Archiv für Anatomie, etc., 1861, p. 653. Herr Babuchin, however, records a shock of Mormyrus (Centralbl. etc., *loc. cit.* p. 163). Goodsir communicated to me his surmise (if he has printed it, I know not) that the pseudoelectric organs of the common skate are electrically active only during sexual excitement.

[1] Archiv für Anatomie, etc., 1858, p. 213.

[2] Comptes rendus, etc., 1865, vol. lxi. p. 239; Journal de l'Anatomie et de la Physiologie, etc. By M. Ch. Robin 2me Année, 1865, pp. 507, 577.

[3] '*Ainsi dans l'appareil électrique des raies, comme sur le Gymnote et le Malaptérure, le courant est constamment dirigé de l'extrémité céphalique vers l'extrémité caudale*' (i. e. in the wire of the multiplier). '*La direction du courant montre que le pôle positif est toujours vers sa partie antérieure, et le pôle negatif vers sa partie postérieure.*' Journal, etc., *l. c.* p. 588).

[4] Histoire Naturelle du Sénégal, Adanson. Paris, 1757, p. 135.

[5] Philosophical Transactions, etc., 1773, p. 461.

[6] Ibidem, 1776, p. 196.

[7] L'identità del Fluido elettrico col così detto Fluido galvanico vittoriosamente dimostrata, etc. Pavia, 1814, 4°. p. 141, § 111.

[8] Philosophical Transactions, etc., 1829, p. 17.

laid down as the first principle of the science of electricity, the identity of all electricity, whatever be its origin; but as regards the five electricities — Voltaic, friction, magneto-, thermo-, and animal electricity—in enumerating the eight effects which ought to be obtained in order to prove their identity, Faraday was compelled in the case of animal electricity to leave four blanks, viz., the spark, thermic effect, attraction and repulsion, and conduction through hot air [1]. Since then, the three first of these effects have been obtained in the Torpedo, and in part by Faraday himself, in the Gymnotus, and the whole position of the matter is such that no one would seriously doubt that the electricity of the Malapterurus is also ordinary electricity. I thought, nevertheless, that I ought not to let the opportunity slip, to complete Faraday's table as far as possible for this fish also. A part of the experiments to be described were made with simple metal saddles, and not with the leading-off cover. As they would have been completely successful with the covers, I have not needlessly hampered the description of them by an account of the mode of leading-off used each time.

1. *Electrolysis.*

The physiological effect and the deflection of the magnetic needle have been already spoken of. Concerning electrolysis, I first observed, with aid of the frog-interrupter, polarisation of the electrodes by the shock of Malapterurus. This observation is so far of importance, as it enabled me to dispense with the decomposition of water, which latter has been unsuccessful in my hands, if indeed it has succeeded in any other [2].

In the electrolysis of iodide of potassium, the remarkable circumstance presented itself, which must have been overlooked by observers of the Torpedo and Gymnotus, that a patch appeared under each point. The two effects, polarisation and secondary iodine patch, which are so closely connected together, were made by me the subject of a special investigation which will be found in the following paper. It was here particularly that the frog-interrupter rendered me help which could scarcely otherwise have been obtained.

In order to observe the decomposition of water, I enclosed two

[1] Experimental Researches, etc., vol. i. London, 1839, p. 99 sq. Series III, 1883, § 351 sq.

[2] John Davy states that he decomposed water with gold and platinum wires (Researches, physiological and anatomical, etc., vol. i. p. 15), Saint-Linari with iron wires (Bibliothèque universelle de Genève, 1837, t. viii. p. 395).

very fine platinum wires in a guttapercha column, out of which copper wires connected with them projected. I cut through the column vertically to the wires, which now appeared as two platinum points at a distance of 2·5 mm. on the cut surface, moistened the surface with the liquids used by John Davy—sulphuric acid ($SO_4H_2 : H_2O :: 1 : 1$) and saturated solution of common salt—and observed the platinum points with a suitable magnifier. A single discharge of the induction apparatus developed bubbles at the negative point; but all efforts to get the same result with the shock of the fish failed. I succeeded just as little in observing a deposit of copper from a sulphate of copper solution on the negative electrode. I might have tried to replace the positive point by a plate, but I did not do so.

2. *Relation of the shock of Malapterurus to resistances opposed to it. Its striking distance.*

The attempt failed completely to conduct the discharge through two copper plates 75 mm. long, 40 mm. broad, which stood opposite each other at a distance of 1–3 mm. in the flame of a Berzelius' lamp; in the experiment, Hankel's flame-currents showed themselves in the galvanometer [1].

I never succeeded in seeing the discharge pass over the smallest gap between stationary metallic conductors with the formation of a spark. I was indebted to the kindness of my friends, Messrs. Siemens and Halske, for a spark-micrometer, in which I could make two platinum points approach each other up to 0·0100 mm.; I also made slits with a knife in strips of tinfoil stuck on microscope slides, which were not wider than 0·0033—0·0050 mm. I never succeeded, whilst observing with the microscope in the dark, in getting a spark from the Malapterurus.

On the other hand, I found to my surprise, that the secondary current of the induction apparatus passed over this slit with formation of sparks, even when the secondary coil was at 90 mm. distance from the primary coil. But my surprise increased still more, when it was found that these discharges caused no sensation either between handle-electrodes, or even on the tongue, although the sparks continued to appear. Even gastrocnemius muscles in the

[1] Poggendorff's Annalen, etc., 1850, vol. lxxxi. p. 213:—Elektrischen Untersuchungen, Ueber das Verhalten der Weingeistflamme in elektrischer Beziehung. (Aus den Abth. d. math.-phys. Classe d. Kgl. Sächsischen Gesellschaft d. Wiss.). Leipzig, 1859.

circuit remained unexcited. If their nerve was in the circuit, twitches presented themselves, as also when the nerve of a nerve-muscle preparation was placed on a gastrocnemius included in the circuit, though the muscle did not itself twitch. But the latter twitches were of unipolar origin, as it was easy to prove[1]. On frequent repetition of the experiment, and especially if the shocks were somewhat strengthened, the slit easily fused together.

In these experiments, the discrepancy which had always been observed between the strength of the shock in Malapterurus as otherwise tested, and its striking distance, manifests itself afresh, and if I mistake not, more clearly than hitherto. It was ever a matter of surprise that such a powerful shock as that of Gymnotus should show itself so sensitive to hindrances in its path, that it will not pass through flame[2], nor even through loosely hanging chains of one of the baser metals, and that it is scarcely perceived with dry copper handles[3]. On account of this behaviour, the identity of the force emanating from electrical fishes with ordinary electricity, was doubted for a long time, and Cavendish sought in vain to remove this difficulty in those theoretical investigations which were far in advance of his time, in which he compared the shock of the electrical fish to that of a battery of great capacity but small tension, which also does not pass readily through a chain[4].

I now give the direct proof of the incomparable superiority, as regards striking distance, of the shocks produced by our apparatus to those of the electrical fish. I am also in a position to give the solution of this enigma, which has escaped all earlier investigators of such fish.

Let two equal currents $I_a = I_b$ flow into two conductors A and B of the resistance λ. Let the ends of the conductor B be connected by a side conductor of the resistance λ_1, whilst the conductor A forms a part of an unbranched circuit. If the resistance λ of the two conductors is increased by the same magnitude δ, it can be shown that I_b loses thereby more than I_a in strength. Let E be the electromotive force in the unbranched circuit, of which A forms a part, let n be a constant > 1, and w the actual resistance in both circuits, then we have

[1] Untersuchungen, etc., vol. i. p. 423 ff.

[2] Humboldt in Observations de Zoologie et d'Anatomie comparée, etc. Paris, 1811, 4°. p. 84.

[3] Faraday, *loc. cit.* p. 5, § 1760.

[4] *Loc. cit.* pp. 217–222, 224, 225. Comp. Untersuchungen, etc., vol. i. p. 563.

$$\frac{E}{w+\lambda} = \frac{nE \cdot \lambda_1}{w\lambda_1 + w\lambda + \lambda\lambda_1}.$$

If we add δ to λ on both sides, we get

$$\frac{E}{w+\lambda+\delta} \gtreqless \frac{nE \cdot \lambda_1}{(w+\lambda_1)(\lambda+\delta) + w\lambda_1}.$$

If we put for n its value from the above equation, the left side of the inequality is found to be the greater.

The proof may also be got at by differentiating with respect to λ the expressions

$$I_a = \frac{E}{w+\lambda} \text{ and } I_b = \frac{nE \cdot \lambda_1}{w\lambda_1 + w\lambda + \lambda\lambda_1},$$

and thus obtaining the quotients

$$\frac{dI_a}{I_a} \text{ and } \frac{dI_b}{I_b}.$$

Without regard to the sign, the latter is the greater; and by both methods one finds that the difference in favour of the conductor *A* is so much the greater as the actual resistance w is greater.

This is an illustration of what occurs in comparing the sources of electricity of our laboratories with the shocks of electrical fish. In those we avoid short circuiting as carefully as possible; in the electrical fish, even when removed from the water, there is always derivation through the body (see above, p. 380). As I emphatically remarked in my first work, its shock is always obtained by derivation[1]. The actual resistance of the organ is very considerable. Consequently an induction shock with a comparatively inconsiderable diminution of strength, can bear much greater resistance than that of an electrical fish of equal or even of much greater strength. Thence may be derived the important rule in experimenting with electrical fish, not to be deceived by the great actual resistance, but always to diminish the resistance of the experimental-circuit as far as possible. This is also the reason of the usefulness of an apparatus, which, like the leading-off covers, diminishes derivation in the experimental circuit as far as possible.

3. *Passage of Sparks.*

In order to observe sparks, the experimental circuit must be opened suddenly at the instant of the shock and as nearly as possible

[1] Vorläufiger Abriss, etc. Poggendorff's Annalen, etc., 1843, vol. lviii. p. 30. § 76.

when it is at its acme. Faraday attained this originally in the simplest manner, by fastening a file to each of the saddles on the Gymnotus, and rubbing one file along the other. He afterwards made use of a toothed-wheel, the circumference of which was rubbed by a spring[1]. I imitated this mode of experiment, at first by making use of a Savart's wheel of 400 teeth, turned by hand 3–4 times in a second. Then, in order to be relieved of the trouble of turning, I took a small toothed-wheel of 50 teeth, which was turned 9–10 times in a second by clock-work, constructed by Herr Grüel, for experiments with colour discs[2]. The spark due to the shock of the Malapterurus was perceived tolerably often in both ways, better however, as far as could be judged, with the Savart's wheel than with the smaller wheel. Perhaps this resulted from the 3–4 times greater number of interruptions with the Savart's wheel; more probably, according to the principle stated above, because the slighter contact of the spring with the teeth and the inferior conduction in the axle-bearings in the case of the small toothed-wheel, weakened the shock more than with the Savart's wheel.

As the frog-interrupter with a sufficient overweight breaks the shock at about the middle of its course, it ought to furnish a new, and, as it seems, the surest mode of observing separation sparks. I have not yet pursued this thought sufficiently. In the few experiments carried out with this object, the place between the point and the plate on which it rests is, in the present form of the interrupter, so unfavourable for observation that no conclusion can be drawn from their failure.

4. *Induction.*

If a coil of 720 turns of copper wire 1·1 mm. thick, the interior of which was 25 mm. wide, and was filled with soft iron wires, was put into the circuit, the extra current naturally made the sparks much stronger.

Induction in a secondary coil by the shock of the fish had never, so far as I know, been before noticed, and it gives the opportunity for an instructive observation. When the shock was sent through the primary coil of a Ruhmkorff's inductorium, the divisions of which were connected so as to have half the length and double the thickness, an observer, placed between copper handles in the circuit of the secondary coil, received a shock. If the platinum

[1] *Loc. cit.* p. 7. § 1767.
[2] Poggendorff's Annalen, etc., 1848, vol. lxxv. p. 525.

points of the spark-micrometer were put in the latter circuit, two sparks, one larger, immediately followed by a smaller, were seen to pass regularly between the points. As these experiments were still made without the frog-interrupter, it is possible that the two sparks may have proceeded from two different shocks, but the regularity of their appearance leads me to believe that they belonged to the beginning and ending current, which corresponded with the rise and fall of one and the same shock. But it is interesting and important, that in accordance with the above principle, we can in this manner obtain from the fish a current which passes over a gap between fixed metals. That this principle actually prevails here, seems to follow from the circumstance, that the sparks failed to pass when the lengths of wire of the primary coil were connected, so as to have double length and half thickness.

5. *Magnetisation.*

The effect of the introduction of the wires in the coil used for obtaining the passage of the spark is to be attributed to the electro-magnetisation of soft iron.

Six completely unmagnetised sewing needles 37 mm. long, 0·7 mm. thick, separated from each other by wax, were put in the hollow axis, 8 mm. wide, of a coil which consisted of 735 turns of a copper wire, 0·4 mm. thick. Three shocks of Malapterurus sufficed to magnetise the needles decidedly strongly, though not to saturation. Ten single opening shocks of the ordinary induction apparatus (one Grove, with the coil quite pushed up) did not make the needles perceptibly magnetic; this was only accomplished when the spark-current had passed for some time through the coil. This current was, however, somewhat more effectual than the shock of the fish.

6. *Electrical Attraction.*

The surest indication of electricity has always been its longest known effect—electroscopic attraction and repulsion. I pass over my unavailing experiments, which were however not long continued, to charge a Leyden jar or a condenser by the fish. Since then, this task has been very perfectly accomplished by Armand Moreau with the Torpedo[1]. But I frequently observed the electrical attraction of two gold leaves by the electricities of the shock

[1] Comptes rendus, etc., 1862, vol. liv. p. 963: Annales des Sciences naturelles, 4ème Série, Zoologie, 1862, vol. xviii. p. 11.

of Malapterurus in the beautiful manner indicated by Mr. Gassiot[1]. The above-mentioned spark-micrometer was so arranged that, in place of the two platinum points which approached each other, two copper wires bent like a swan's neck were used, from which gold leaves hung down opposite each other. A glass case shielded it from any draught. At a distance of 3 mm. from each other, the movement of the leaves at the moment of the shock was doubtful. At a distance of 2 mm. they obviously attracted each other. At a less distance they flew together, a magnificent green flash appeared and left the leaves fused together. It was then often possible to tear them asunder uninjured by means of the micrometer screw, and to repeat the experiment.

Unipolar action, to be discussed in Sect. 3 of the following paper, is concerned here.

8. More detailed Investigation of the distribution of tensions in the active organ of Malapterurus. The posterior half of the organ acts more feebly than the anterior. The Equator of the organ.

It is the custom to speak of the polar surfaces of the electrical organs. This is however a mistake, unless the organ is cut out of the animal, raised into the air, and regardedas endowed with equal electromotive forces at all points. As long as the organs are under water, or are adjacent laterally to animal parts which have similar relations as conductors, there can be no question of polar surfaces in the strict sense of the word. If we represent such an organ diagrammatically as a cylinder, the current curves now cut the coat of the cylinder, instead of issuing only from its basal surfaces. We may, nevertheless, speak of the polar surfaces of the organ with the same accuracy as we do of those of a magnet, and with this proviso we shall make use of this mode of expression. Minuter details as to the special distribution of the discharge of the electric fish will be found in my Collected Papers, No. XXX.

[1] On the attraction force manifested by the electricity of the Gymnotus electricus. In the Transactions and the Proceedings of the London Electrical Society, from 1837 to 1840. London, 1841, 4°. p. 197. Matteucci had described a similar experiment on the Torpedo somewhat earlier. A wire supports the one gold leaf above the edge of a metal disc, on which the fish lies. The other is suspended by a similar wire at the edge of a metal cover put on the back of the fish. This cover is moved in order to excite the fish, then the gold leaves may be seen to attract each other (Bibliothèque Universelle, etc. Nouvelle Série, 1837, t. xi. p. 392; Essai sur des Phénomènes électriques des Animaux, 1840, p. 51, Fig. V; Traité, etc., p. 154, pl. III. Fig. 27). It is difficult to comprehend how one can judge of the attraction of the gold leaves, when one moves them one's self and moreover in the open air.

With the help of a pair of platinum electrodes, to which a telegraph wire insulated with guttapercha served as a handle (see above, pp. 380, 381), I readily observed that any point of the organ nearer the tail behaves positively to any point nearer the head, no matter where the point may lie on the circumference of a given transverse section of the fish, whether on the back, flank, or belly. The fish allowed a strip of platinum to be pushed quietly from the flank under the belly without giving a shock, and only discharged when the other electrode was put on it.

It follows from these experiments, that the polar surfaces of the organ lie at the head and the tail, and on account of the tubular shape of the organ, the poles themselves must be sought somewhere in the body of the fish within the annular anterior or posterior limit. It follows further, that the shocks must increase with the distance of the contacts in the fish, or as we call it in muscle or nerve, with the span of the leading-off arch. The result confirmed this surmise. On a large Malapterurus I placed two zinc saddles, first at a distance of 1 cm., then of 2 cm. from each other at their inner edges, then so that the contacts were at the ends of the organ, finally so that they touched the mouth and tail. I obtained deflections of 20, 50, 116, 140 sc. respectively. In the last experiment the fish gave two shocks, and, as I still worked without the frog-interrupter, it remains doubtful whether the greater strength of the effect was due only to the double shock, or also to the greater difference of tension between the points from which it was led off.

These facts had been already observed by Ranzi in Malapterurus (see above, p. 388, note 2), and perfectly similar ones by Faraday in the Gymnotus, but with reversed signs. But whereas De la Rive remarks expressly that the anterior and the posterior halves of the organ of Gymnotus discharge with precisely equal strength[1], it was found in Malapterurus that the anterior half of the organ exceeds the posterior half in activity, and indeed in the ratio of 11 : 6. This ratio is very regular under ordinary circumstances, as will be seen from the numbers to be given immediately.

When I first met with this difference, I imagined that it must be due to a difference of structure, perhaps to a difference in the number of plates in a unit of length. But I convinced myself, in common with Max Schultze, that nothing of the sort exists[2]. Then

[1] Archives de l'Électricité, 1845, vol. v. p. 505; Traité de l'Électricité théorique et appliquée, etc., vol. iii. Paris, 1858, p. 76.

[2] Comp. M. Schultze in the Abhandlungen der naturforschenden Gesellschaft in Halle, etc., *loc. cit.* pp. 16, 17.

I considered whether the less strength of the posterior half might not depend on the distribution of a single nerve-tube in the whole organ, in consequence of which, the wave of innervation would be weakened before reaching the posterior part of the organ.

However, before such a theory of the phenomenon can be propounded, another question must be solved. Does the posterior half of the organ act with less electromotive force than the anterior, or does the feebleness of its action result simply from its smaller transverse section, and consequently greater resistance? Not only is the organ somewhat thinner at the tail, but the diameter of the tube formed by it decreases. The organ indeed decreases somewhat in transverse section towards the head also, but much more gradually.

It seemed possible to decide by experiment the question, whether this is the reason of the behaviour observed. I prepared a leading-off cover, which had a third lining in the middle of its length, and determined the relation of the shock proceeding from the two halves, both with small and great resistance in the experimental circuit. In the latter case, the circuit contained a tube 142 mm. long, 1·6 mm. wide, filled with distilled water, to which some spring water was added. The bobbins of the galvanometer (12,000 turns) were obliged to be close up in order to obtain perceptible deflections. The frog-interrupter worked with an overweight of 100 gr. in this and in all the following experiments, where it is not otherwise stated. With only an instantaneous excitation, this would correspond to about 0·0168″[1], according to Helmholtz' determinations; but I have already before explained the reasons why these determinations are not directly applicable[2]. The number of shocks indicated by the frog-alarum every time the cover was put on, although always recorded in my note-book, is omitted in the following tables, because when the frog-interrupter is used, it makes no difference.

Resistance.	*Half of the Organ.*	1	2	3	4	5	6	7	8	9	*Mean.*	*A : P.*
Small	Anterior (A)	25		22		19					22	=100:54·55, or=11:6.
	Posterior (P)		12		14		10				12	
Great	Anterior (A)		5		7		8		10		7·5	=100:93·33.
	Posterior (P)	5		8		6		7		9	7·0	

[1] Archiv für Anatomie, etc., 1850, p. 325.
[2] Ges. Abhandl., vol. i. pp. 226, 227.

Thus, with increasing resistance of the experimental circuit, the ratio between the effects of both halves actually approaches to unity. There would be no reason for this if the different strengths of the shocks of the two halves were occasioned by difference of electro-motive force, and we may therefore conclude that the less activity of the posterior half of the organ is due to greater resistance.

I succeeded in demonstrating the superiority of the anterior over the posterior half of the organ in another very instructive manner. I fixed two zinc saddles on to one of the fish at such a distance from each other, that they corresponded to the poles of the organ, and I made a third saddle movable in such a way that it could divide the distance between the two first (125 mm.) in any desired proportion. The middle saddle was connected by the frog-interrupter with the one terminal A, and the two other saddles were connected with the other terminal B of the galvanometer, the thermo-bobbins of which (212 turns) were close up. With this arrangement, each of the two sections of the organ sent a current in an opposite direction through the galvanometer. I now tried to give such a position to the middle saddle that both currents should be equal, or that the mirror should remain at rest. The results of the experiments are shown in the following table, in which a deflection in the direction of the anterior half is denoted positive and of the posterior negative :—

Ratio of length of the anterior section to the posterior.	*Effect on the galvanometer.*
62·5 : 62·5	Positive deflection, not measurable.
50 : 75	+42 scale divisions.
45 : 80	+22; −3; +23.
40 : 85	Strong negative deflection.

The ratio 45 : 80 seemed nearest to that sought. In order to learn to what extent the equilibrium found was complete, the effect of the anterior section, 45 mm. long, and of the posterior, 80 mm., was measured separately, with only 53 turns. The former was found = + 48, or multiplied into 4 = + 192; the latter = − 34, or multiplied into 4 + − 136 sc. Equilibrium was certainly attained as nearly as possible, when the difficulty of the experiment is considered.

This experiment acquaints us with the equator of the organ, or

its neutral transverse section in presence of the leading-off cover, but independently of the branch-current through the galvanometer. The resistance of the conducting wires leading from the poles to the terminal B of the galvanometer was the same, and thus the mean tension between the tensions at the two poles, i.e. tension zero, prevailed at the point B; consequently, when no current was present in the galvanometer, the tension at the terminal A was also nil, and, according to Bosscha's law, as there was no current in the galvanometer-circuit, its removal would make no difference (see Collected Papers, vol. ii. pp. 83, 84, note).

I went a step further. I put a pair of saddles, having a constant space between them (2 cm. between the edges of the bands opposite each other) on the fish, at different points of its length. I got, as the means of several experiments, the following deflections :—

From the anterior third ..... 26 scale divisions.
„ middle „ ..... 29 „ „
„ posterior „ ..... 13 „ „

Thus the curve of the tensions, the axis of the fish being taken as the axis of abscissae, rises almost in a straight line from the front backwards as far as the end of the middle third, and then becomes convex towards the axis. It follows also from this, that the equator is shifted towards the anterior end. Whether the somewhat smaller amount of the deflection from the anterior third, in comparison with the amount of the deflection from the middle third, was due to the diminution of the transverse section of the organ towards the anterior end (p. 399), or whether it was accidental, I cannot say.

I prepared a cover like the former one, except that all the gutta-percha between the three linings was removed except three narrow strips, one on the back and one on each side. In this case, the ratio A : P ought to be greater than with the complete cover. I obtained the following result :—

Half of the Organ.	1	2	3	4	5	6	7	8	9	10	*Mean.*	*A : P.*
Anterior	36			31		35		33		19	30·8	= 100 : 54·55,
Posterior		14	12		14		21		12		16·8	or 11 : 6

The experiment, as is seen, was a failure, inasmuch as the ratio 11 : 6 recurred with remarkable exactness. Evidently some chance

came into play, for such uniformity is not to be thought of here. Unfortunately I never repeated the experiment, and therefore a certain obscurity is left in this respect also.

9. On the influence of the length of the linings of the leading-off covers upon the strength of the branch current in the experimental circuit.

A series of experiments have their place here, the object of which was to determine the most favourable conditions for the construction of the leading-off cover. The question is the length [1] to be given to the linings. In Fig. 10, these have a medium length which was given to them by guess. But the length of the linings affects the strength of the branch current in the experimental circuit in a two-fold way. First, its strength increases with their surface, inasmuch as this increase of surface diminishes the resistance of the circuit. Secondly, if we suppose the linings not in electrical connexion to be applied to the electromotive surfaces of the organ, it is clear that the tensions of the latter will in part equalise themselves through the linings. Thus the strength of the current in the experimental circuit will be directly proportional to the mean tension of the surface touched by them, and inversely proportional to the resistance of the experimental circuit. Accordingly, it seems as though, when the resistance of the experimental circuit is greater, shorter linings would be more advantageous, and longer when the resistance is less: and in order to obtain the strongest possible effect from the fish under different circumstances, I undertook to decide this question by experiment.

Of two covers fitting the same fish, I provided the one with short, the other with long linings. In the latter case, a gap of only 8 mm. was left between them; the short linings were about 2 cm. wide. With these linings it was easy to prove [2] the correctness of the above conclusion. The great resistance here was a tube 280 mm. long, 1·4 mm. wide, filled with solution of sulphate of zinc, and it was again necessary to push the bobbins of the galvanometer close up (see above, p. 400).

[1] Comp. Ges. Abhandl., vol. i. p. 215.

[2] These experiments also were not performed until after the lecture in the Academy, where I could only express the surmise that this would prove to be the case. (*Loc. cit.* p. 104.)

Small resistance.

Lining.	1	2	3	4	5	6	7	8	9	10	11	*Mean.*
Long ...		74		50	64		41		40		40	51·5
Short...	20		57			28		37		30		34·4

Great resistance.

Long ...		54		75								64·5
Short...	73		74		100							82·3

If shocks were taken from the fish alternately with covers with long and short linings, the greater strength of the latter was very clear.

10. More precise examination of the value of the Frog-interrupter in experiments on the Malapterurus.

I do not return here to a detailed consideration of the questions as to the time relations of the shock, but refer to what has already been said on this matter in discussing the frog-interrupter, p. 385.

In the 'Description of certain Apparatus and Methods of Experiment,' it was shown that the frog-interrupter serves the purpose of opening the circuit at any required short period after the excitation with sufficient accuracy. Consequently the great irregularities which were always observable in the effects of the shock of the fish were the more obvious. They finally led me to decide on testing the action of the interrupter in experiments on the fishes themselves also, although it seemed inconceivable that it should not do here what was expected from it.

At first, I simply made series of experiments with increasing overweight, in order to see how the deflections caused by the fish shock would increase correspondingly to the overweight. Thus I obtained (with 53 turns at 75 mm. distance) the series immediately following, in which W.I. signifies 'without interrupter.'

Overweight.	2 *gr.*	*W.I.*	2	50	100	150	200	*W.I.*	250	300	350	450	500
I.	8·2	125	10·7	8·4	16·3	17·8	25·0	80	—	—	—	—	—
II.	—	—	—	8	8·8	10·0	9·0	—	14	14·6	24·8	22·6	22

The fall of the deflections at the close of the second series may be explained thus: at the time of the interruption, a great part of

the shock was over, consequently the fatigue of the fish was more influential than the prolongation of the time of closure by increasing the overweight.

But I now began other series of experiments, in which I proposed to prove directly, the regularity introduced by the frog-interrupter into the results of the fish experiments. I wished to show that the mean error of a series of deflections caused by the fish was diminished by the frog-interrupter. With this object, I made the wires proceeding from the cover, divide into two conductors, the one of which led to the galvanometer, guarded as usual by the frog-interrupter, and the other led to an unguarded galvanometer. The guarded galvanometer, until its circuit was opened, weakened the current in the unguarded one. However this could have no other effect on the result, than to make the deflections in the unguarded galvanometer still more irregular. I made only one such experiment, but it was unsuccessful, inasmuch as the guarded galvanometer, for some incomprehensible reason, gave less regular deflections than the unguarded one. Soon afterwards the last of my fishes died, and I remained in the dark as to the reason of failure.

11. Of the relative immunity of Malapterurus from electric shocks.

As long ago as 1842, in my 'Vorläufiger Abriss,' I discussed the question[1], how it happens that an electrical fish strikes other fish to death, but neither itself nor, according to v. Humboldt's[2] and Colladon's[3] experience its fellows; why the Torpedo, which is viviparous, does not kill the young in its uterus? I was led to this question by the consideration, that according to indubitable physical laws, the shock of necessity passes through the body of the fish itself, in fact that this body is more favourably situated in regard to the organ for the reception of the shock than the body of another animal approached by it.

This statement might perhaps be doubted in regard to the Gymnotus, on account of its head being so far in front of the anterior polar surface of the organ. It is certainly correct in the case of the Torpedo, and it is hardly invalidated by the remark,

[1] Poggendorff's Annalen, etc., 1843, vol. lviii. pp. 29, 30, § 75.

[2] Recueil d'Observations de Zoologie, etc., p. 80.

[3] Comptes rendus, etc., t. iii. p. 490; L'Institut, etc., t. iv. No. 181, p. 350; Poggendorff's Annalen, etc., 1836, vol. xxxix. p. 413.

that the accumulated discharges of both organs strike the central nervous system vertically to its axis. But the truth of the statement is not so obvious in any of the three electrical fishes as in the Malapterurus.

Nevertheless, I did not omit to put it to the test of experiment, and to prove that the discharge actually goes through the body of the fish. For this object, I put insulated copper wires into the body through the mouth and vent of a Malapterurus doomed to death, while an assistant held it with an indiarubber glove. When it was placed in a small parallelopiped glass trough full of water, with the wires in its body, and its skin was excited with a glass rod, it discharged, and the current always showed itself in the circuit of the wires in the right direction and strength.

The only conceivable reply to the question, why the electrical fish does not kill itself, was evidently that it is very little or not at all sensitive to electric shocks. I had made in the year 1852 experiments with Faraday on the Gymnotus of the *Polytechnic Institution*, in order to discover if the fish is as insensitive to currents of external origin as to its own. We did not succeed in exciting the fish perceptibly; however it was found that generally even in a man, our apparatus was too weak to produce any appreciable effects[1] in the large mass of water which contained the animal.

I was now naturally very eager to obtain from the Malapterurus the reply to this question, which had been in my mind for fifteen years. With this object, I let down into the water of the experimental tub, a pair of zinc electrodes as the terminals of the secondary coil of the induction apparatus, and in addition, for a reason to be explained immediately, a pair of platinum electrodes in connexion with half of the length of the nerve multiplier. Two Groves were placed in the primary circuit of the induction apparatus. As I had expected, the multiplier was not affected by the alternating currents of the inductorium, as the current from it was too weak to produce a deflection in successively opposite directions.

When I put into the tub, river-fish of this country, tench, perch (*Perca fluviatilis*), chub (*Carassius Gibelio*), burbot (*Lota fluviatilis*), pike (*Esox Lucius*), Silurus (*Silurus Glanis*), and exposed them to the current, they tilted over on their side when the coil was pushed up half-way, did not move their gills any more, and drifted about unconsciously. If this condition was allowed to continue,

[1] Comp. above, p. 380, and Ges. Abh. vol. ii. xxx. § 4.

the fish died; some sorts of fish were more easily killed than others. Frogs were strongly tetanised, but recovered easily[1].

Now, if I put a Malapterurus in the tub instead of or along with the fish, it behaved in a very different manner. By the shocks which sufficed for the fatal stupefaction of the other fishes, it appeared to be unaffected, just like a frog in a Guericke's vacuum as compared with a guinea-pig or a linnet. If a fish or a frog came too near it, it also discharged its battery, as was indicated by the multiplier needle which was thrown against the stop and the astaticism of which was destroyed. The only perceptible effect of the shocks upon the Malapterurus was, that on opening the key, its barbels were laid back, and it is worthy of remark, that the barbels of the Silurus also move in a similar way when it is tetanised. However, when the utmost force was imparted to the shocks, by pushing the coil fully up, it was easy to see that the fish noticed and avoided them. If it came in the neighbourhood of the electrodes, where the current density was greatest, it withdrew hastily, gave a shock or two, and sought with correct instinct, that position in which its axis of length cut perpendicularly the least dense current curves, as if it knew the laws of the distribution of current in non-prismatic conductors. But it moved gills and fins with usual rhythm in the midst of the strongest currents, and swam out of their range without a single convulsive or involuntary movement.

Tin electrodes in connexion with the induction apparatus, and platinum electrodes in connexion with the half length of the nerve multiplier, were put on a dying Malapterurus, which lay in a small parallelopiped glass trough, which it almost filled (see p. 405). Even with two Groves in the primary circuit of the induction apparatus and with the coil quite pushed in, the fish seemed not to perceive the shocks at all, breathed on quietly and did not discharge. A deflection in successively opposite directions now presented itself.

The result was substantially the same with the current of a Grove's battery of thirty cells, in place of the alternating current of the inductorium. The common river fish, whilst the key was shut, lay on their side and their fins twitched. When it was opened, a general convulsive movement ensued, but shortly afterwards, if the current had not lasted too long, they swam about

[1] Comp. similar experiment by R. Böttger in Poggendorff's Annalen, etc., 1840, vol. l. p. 39.

again. Tetanising evidently affected them more than the current of comparatively constant density. The Malapterurus withstood the effect of the constant current also, and this appears to be of special interest, as it did not need to be accommodated to it. However, here also, it sought that position which is theoretically the most protected.

It is now clear why the Malapterurus does not suffer from its own current, and the same reason will naturally hold good for other electrical fish. They all possess, at all events relative immunity[1] as regards electric currents, for the exposed muscles and muscle nerves of electrical fishes, and even the electrical nerves themselves are excitable by the current, and consequently their immunity must have a limit of current density inferior to that attained in experiments. It would certainly be possible to kill a Malapterurus with a Leyden battery of a certain size, if it were charged to sufficiently high tension. Wherever this limit may lie, the difference between electrical fish and other animals is great enough to be regarded as one of the most enigmatical facts of physiology. According to ancient accounts, crabs are said to possess immunity as regards the shock of the Gymnotus[2]. I therefore subjected the cray-fish of this country to the same experiments as the fish and the frog. It is true that they bear a great deal, perhaps because their chitine tunics protect them. When they are tetanised, they twitch violently, their body is contorted, their antennae are laid back, but there is no such immunity as that of Malapterurus. I need not refer to the well-known, and in part very naïve tales concerning the immunity of certain men from electric shocks[3].

[1] In M. Colladon's paper on the Torpedo, we read (p. 491): 'M. J. Davy a constaté ... que le courant d'une pile ne paraît pas faire souffrir ceux de ces poissons qui sont interposés dans le circuit.' This is a misunderstanding of Colladon's. John Davy's statement about the absence of influence of the current on the Torpedo refers solely to the electrical organs, and only assists him to conclude that the organs are not muscles. (Philosophical Transactions, etc., 1832, p. 269; Researches, physiological and anatomical, London, 1839, vol. i. pp. 32–34.)

[2] Priestley, The History and present state of Electricity, London, 1769, p. 403. G. H. Loskiel, Geschichte der Mission der evangelischen Brüder unter den Indianern in Nordamerika, Barby, 1789, p. 124; also in Voigt's Magazin für das Neuste aus der Physik, u. s. w., Gotha 1789. Bd. VI. St. ii. S. 171, Loskiel's statement appears the more questionable, as there are no Gymnotus in North America. Alex. v. Humboldt produced convulsive movements in crabs on the Lido by the simple battery (Versuche über die gereizte Muskel- und Nerven-faser, Berlin und Posen, 1797, vol. i. p. 285.)

[3] Comp. Humboldt, Versuche über die gereizte Muskel- und Nerven-faser, u. s. w., vol. i. p. 160; Recueil d'Observations de Zoologie, etc., p. 69.

There are many instances on record of the immunity of certain animals from certain injurious agencies which are destructive of most others. I have collected a large number of such accounts, but it would lead us too far from our object to mention them in detail, the more so, that they are often very indefinite and not well authenticated. Teleologically, the comparison with the immunity of vipers from their own poison, proved by Fontana, is the nearest. Although Fontana had shown that non-poisonous snakes, lizards, toads, eels, snails and leeches are also proof against the viper's poison like the viper itself, yet the immunity of the viper suggested the notion and afforded support to it, that animals are fundamentally proof against a poison produced by themselves. But this is not always the case. Fontana had already remarked, that animals with corrosive and acid secretions, like the hymenoptera are not proof against their own poison[1].

And this brings us to the point with which we are here concerned. All those immunities relate to substances acting in a specific manner, and which can therefore be resisted by a specific organisation. That strychnine in such small amounts kills most animals, is at bottom more remarkable than that the fowl[2], the rhinoceros bird and the sloth[3] can resist it more or less. But immunity from a natural power like electricity, gives at first sight almost the impression as if an animal were proof against a corrosive or a metallic poison, against mechanical force or destructive heat.

This is however a deceptive appearance. The electric current stands to nerve and muscle in as peculiar a relation, as according to modern ideas, certain organic molecules do to certain limited provinces of the nervous system, and it is ultimately not more wonderful, that in this special relation variations occur in the case of certain animals, than that other animals are relatively proof against the strychnine molecule which is so formidable to all others. Along with the effects which the current produces in animals, in virtue of its special relation to nerve and muscle, it is capable of other, more general effects, which, if increased beyond a certain degree, become likewise destructive to the animal in its thermic, electrolytic, cataphoric and anaphoric actions. That electrical fishes are not exempt from these actions is clear. This consideration does not in the least detract from the importance of

[1] Abhandlung über das Viperngift, u. s. w., Berlin, 1787, 4°. p. 15 ff. p. 155.
[2] Lehube in the Archiv für Anatomie, u. s. w., 1867, p. 629.
[3] Ibid. 1868, p. 756.

the problem, of the immunity of electrical fish from the electric current. On the contrary, it affords us an additional motive in our efforts to solve it, in as far as it opens the prospect, that disclosures of importance in relation to the general physics of muscle and nerve will result from it.

Pflüger, who was a witness of my experiments (see above, p. 387), and who at that time was working at electrotonus, conjectured that the Malapterurus may have power to put its nerves into a state of anelectrotonus. But except under the influence of extraneous currents, no trace of electrotonic conditions has ever been observed in the nervous system. Pflüger's theory seems to be contradicted also by the following experiment. The electrical nerve of the dying Malapterurus in the glass trough (see above, p. 406) had been ligatured, and therefore could no longer be anelectrotonised by means of its giant ganglion cells. Notwithstanding, it was not excited by very strong alternating currents.

There might be supposed to be some connexion between the immunity of electrical fishes from the current, and the much discussed inexcitability of the spinal cord. This would be quite arbitrary, for the same electrical nerve, which in the previous experiment showed itself electrically unexcitable, gave a violent shock at the moment of ligaturing the nerve, and in another experiment, section acted in the same way. The spinal cord, on the contrary, responds as little to mechanical as to electrical irritations.

Since Brücke showed that muscles with the nerve removed, are little sensitive to currents of short duration[1], the fact that the Malapterurus is also proof against the constant current of a battery assumed much greater importance (see p. 407). Its immunity is therefore not, like that of the muscles, connected with the duration of the current.

No other opinion seems to me to be left open, than that the threshold of excitation lies higher for the nerves of the electrical fish than for the nerves of other animals. I should have continued the investigation further in this direction myself, if opportunity had been afforded to me. I rejoice all the more that Boll has recently followed this track in the case of the Torpedo, apparently with good success[2].

[1] Sitzungsberichte der Wiener Akademie, u. s. w., 1867, vol. lvi. Part ii. p. 594; 1868, vol. lvii. Part ii. p. 125; Vorlesungen über Physiologie, 2 Ed. 1875, vol. i. p. 485.

[2] Archiv für Anatomie, u. s. w., 1873, p. 76. According to Steiner, the threshold of electrical excitation in the Torpedo would lie below the thickness which a shock of

12. Experiments on living electrical nerve and organ after separation.

The following experiments were made on a dying Malapterurus which had been used for several previous investigations.

When the electrical nerve was laid on the platinum plate of the leading-in apparatus[1], and was tetanised, tetanus of a nerve-muscle preparation followed, wherever on the organ of the same side, the nerve was placed. If the stimulation of the electrical nerve is continued, the organ does not produce a continuous current, as one might suppose, but a series of rapidly succeeding shocks, just as the contraction and variation of current in a muscle, which are produced by continuous excitation of its nerve are only apparently constant. It is a proof of the small amount of discernment with which Matteucci conducted his numberless experiments, that he left such fundamental questions for me to answer[2].

The needle of the multiplier, connected with the fish by platinum electrodes, was deflected at the commencement of the tetanus, but took up no fixed position. However, it might be possible that with unpolarisable electrodes and with an aperiodic light magnet, the result would be different. The positive polarisation of the organ by its own current[3] might be matter for consideration. After a few minutes rest, the tetanus was again observed. I find no mention in my diary as to the distance of the secondary coil, at which it occurred.

When a current of two Groves was sent through the nerve nothing resulted. With five Groves, a shock at closing the current took place, which showed itself by twitching of the nerve-muscle preparation, and in the galvanometer, by a deflection in the right direction. The great strength of current required for the stimulation of the nerves was very surprising; however, the nerve was no longer fresh, and it was not possible to make comparative observations. It therefore remained uncertain, whether it might

the Torpedo B, or even of the Torpedo A itself can reach in the Torpedo A, ibid. 1873, p. 684.

[1] Untersuchungen, etc., vol. i. p. 450, Tab. ii. Fig. 20, 21.

[2] Four years later than I, Moreau also stated that tetanising the electrical nerve (in the Torpedo) produces an uninterrupted series of shocks, without saying however, how this was observed (Annales des Sciences naturelles, etc., 4me. Série, Zoologie, 1862, t. xviii. p. 10). This statement was incorrectly regarded as new by the reporters of his work, MM. Claude Bernard and Becquerel senior (Comptes rendus, etc., 1862, vol. liv. p. 966). Comp. also Marey in the Comptes rendus, etc., 1871, t. lxiii. p. 918. See moreover Boll, Archiv für Anatomie, etc., 1873, p. 79.

[3] See Gesammelte Abhandlungen, vol. ii. xxxi. § 6.

be concluded from this experiment that the threshold of excitation for electrical nerves is abnormally high. There was no twitching of the muscles of the trunk, even when the coil was pushed quite up and with two Groves in the primary circuit of the induction apparatus; on the other hand, the muscles of the head and intestine contracted. But, as regards the former, it must be added that they did not respond to the irritation of a saturated solution of common salt either.

After circulation had ceased for $2\frac{3}{4}$ hours, the organ, when irritated through its nerve, acted upon the multiplier; but when irritated directly, either mechanically or with caustic potash, it acted neither upon the multiplier nor upon the nerve-muscle preparation.

The electrical nerve, with its longitudinal and cross section properly laid upon the pads of the nerve-multiplier, failed to exhibit any nerve-current, or on being tetanised, any negative variation. This appears natural when we consider that the nerve consists of a single nerve-tube, which is no doubt unusually thick, but is also surrounded by a disproportionately strong[1] sheath, the effect of which is to efface the electromotive action of the nerve-tube by derivation. It is however conceivable, that a more efficient electrical nerve of the Malapterurus might show traces on the galvanometer of the nerve-current and of its negative variation.

Electrotonic currents were clearly perceived with two Groves; after cutting through the nerve between the stimulated and led-off tract and joining the cut ends, feeble actions in the wrong direction, depending upon escape of current, afforded evidence of the genuineness of the previously observed deflections.

Here, the experiments on the electromotive activity of the organ at rest, and on its secondary electromotive actions come to a close. A more detailed report of both is given in § 6 of the 'Experimental criticism of the discharge hypothesis.'

[1] Bilharz, *loc. cit.* p. 21, states the thickness of the sheath containing the vessel as nine times that of the empty sheath. The diameter of the fibres themselves is to that of the empty sheath in the proportion of 2·6 : 24·6 according to his drawings, *loc. cit.* Tab. iii. Fig. 9. Hence the ratio of the cross section of the fibres to that of the whole nerve is shown to be 1 : 8950. Max Schültze gives the ratio of the fibres to the empty sheath still more unfavourably in his illustration in Fig. 7, Tab. i. of his paper (3·25 : 33·10.)

13. Of the chemical reaction of the electrical organ of the Malapterurus[1].

Max Schultze had stated, when making observations at Trieste, that the electrical organ of living Torpedos has a distinctly acid reaction[2]. I examined the electrical organ of the Malapterurus repeatedly as to its reaction. In the fresh state, I found it neutral according to the manner of the reaction of muscle, i.e. amphoteric[3], and only later, from about the third day forwards, distinctly acid. The red spots did not disappear on drying. On the fourth day (in one case) the organ was decidedly in a state of decomposition, and its reaction was alkaline.

With a fresh organ, on the first day, I examined the effect of higher temperature on the reaction. After keeping it for five minutes in water at 40–50°C., which by the way leaves the consistency of the organ unaltered, the neutral reaction changed to an acid one. In order, however, that this should appear clearly, the organ must be in contact with the litmus paper longer than frog muscles treated in the same way (see Collected Papers, p. 17). A more important difference between organ and muscle is, that pieces of the organ thrown into boiling water become acid, instead of becoming more alkaline like muscles (p. 18). Thus, in this respect, the electrical organ agrees with the nervous central organs, which, according to Funke[4], also become acid at boiling temperature. But whereas Funke considers that brain and spinal cord become more acid at boiling temperature than at 40–50°, the acid reaction of the boiled organ seemed to me less marked than that of the organ heated only 40 or 50°; this might be considered to indicate a transition to the behaviour of muscles.

[1] With use of my 'Bemerkungen über die Reaction der elektrischen Organe und der Muskeln,' in the Archiv für Anatomie, etc., 1859, p. 846. (Comp. above, p. 369.)

[2] Zur Kenntniss der elektrischen Organe der Fische. Zweite Abtheilung, Torpedo, Halle, 1859, 4°. p. 27.

[3] Gesammelte Abhandlungen, note 1 on p. 10. Comp. Kühne in Virchow's Archiv für pathologische Anatomie, etc., vol. xiv. 1858, p. 328, 334, 345, 347. [Heidenhain has since distinguished this kind of reaction from neutral reaction, as amphichromatic (Mechanische Leistung, etc., p. 153.) Recently, it has been called the amphoteric reaction. Comp. Heintz, Ueber die Ursache der Coagulation des Milchcaseïn durch Lab und über die sogenannten amphotere Reaction. Journal für praktische Chemie, 1872, vol. vii. p. 374. It was my friend Heintz, who, in the beginning of my experiments on the reaction of muscles, called my attention to the surmise, that in amphoteric reaction, the blue colour would not become red and the red blue, but that both colours would alike become violet; experiment confirmed this conjecture.]

[4] Archiv für Anatomie, &c., 1849, p. 841. Comp. Gscheidlen, Ueber die chemische Reaction der nervösen Centralorgane. Pflüger's Archiv, &c., 1874, vol. viii. p. 177.

It was certainly in the highest degree improbable, that the fresh organ of the Malapterurus should have an amphichromatic reaction, and that of the Torpedo, an acid one. In order to explain Max Schultze's statement, I therefore ventured the suggestion, that the electrical organ might, like muscle, become more acid by continuous exertion. It is easy to conceive that Torpedos, from the moment of their capture until they reach the observer's hands, are exposed to a multitude of annoyances, to which they respond by shocks, so that they themselves bring their organ into the condition of the muscles of guinea-pigs and frogs which I had tetanised to exhaustion (see Collected Papers, vol. ii. pp. 26 ff. and 716).

This suggestion has only been verified in part. Moreau found that the organ of the Torpedo had a neutral reaction[1]; Boll an alkaline one; thus in any case, Max Schultze is mistaken in regard to the reaction of the fresh organ in a state of rest. After the lapse of 6–10 hours, Boll saw that the organ of the Torpedo had become acid. According to him, however, it does not become acid like muscles, through exertion[2], and thus it remains uncertain how Max Schultze was misled.

[1] Annales des Sciences naturelles, etc., *loc. cit.* p. 6.
[2] Archiv für Anatomie, etc., 1273, pp. 99, 100.

XII.

LIVING TORPEDOS IN BERLIN.

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XII.

1. Introductory.

Until recently it had not been possible, even under favourable conditions, to keep Torpedos alive in captivity more than a few days. On this circumstance was founded the opinion expressed by Faraday five-and-forty years ago, that in certain respects the Gymnotus was better adapted than the Torpedo for researches on electrical fishes[1]; in writing on this subject later I placed the Malapterurus above the Gymnotus as an object of research, observing that 'the Torpedo being a sea fish could not be taken into account[2].' The state of matters has since then entirely altered.

Not only is the art of keeping marine animals in the Aquaria which have come into existence during the last twenty years so much advanced, that there is now no difficulty in preserving Torpedos in a living state as long as is necessary; but also the methods of railway transport are now so perfect that it is possible to convey the inhabitants of the ocean to great distances from the coast without risk. At the very time I wrote the words above quoted, Ranvier had at his disposal living Torpedos from Concarneau on the Atlantic Ocean[3]. It is, however, remarkable that in the exhibition in the Champs Elysées, as well as those in Munich and Vienna, these 'oldest of all electrical machines,' as they were called by George Wilson[4], were wanting; their only representatives being the submarine instruments of warfare which have been called after them.

Torpedos were first received at the Berlin Aquarium in the summer of 1881 from Trieste. The director, Dr. Otto Hermes, who makes the resources of the institution available for scientific purposes with the utmost liberality and courtesy, at that time permitted me to make some experiments. These were, however, limited to such general observations as could be made without interfering with the purpose for which the animals were kept. I have repeatedly on former occasions explained why the possession of

[1] Notice of the character and direction of the electric force of the Gymnotus (1838).
[2] E. du Bois-Reymond, Gesammelte Abhandlungen, vol. ii. p. 611.
[3] Leçons sur l'histologie du Système Nerveux, Paris, 1878, vol. ii. p. 88.
[4] The Edinburgh New Philosophical Journal, Oct. 1857, p. 267.

living electrical fish is under these circumstances not so useful as might be expected[1]. Dr. Hermes, however, was so good as to arrange recently for supplying the Physiological Institute with Torpedos through the Aquarium at Trieste, so that I might be able to make such experiments on them as seemed desirable. It is scarcely necessary to observe what an admirable prospect is thereby opened for the advancement of the knowledge of electrical fishes, and consequently of the physics of nerve and muscle. A single Torpedo at one's disposal in a German physiological laboratory is possibly capable of yielding more for the progress of our science than, to adopt Shylock's mode of expression, the Adriatic full of Torpedos could do at a place where you must first set up a galvanometer, and where, on account of some piece of apparatus left at home or broken in the journey, the most admirable plan of experiment becomes futile.

In this way I have already worked out two Torpedos during last summer, and three during the winter, and by means of them have answered several questions which had been long present to my mind, and I have also begun the observation of the secondary electromotive actions of the electrical organ. Although these last researches are not completed, I publish the results already obtained as, even in their present condition they constitute an important supplement to my previous communication on secondary electromotive phenomena[2]. Moreover, the very small measure of completeness which I was able to give to the researches on the same subject in muscles and nerves did not appear to be attainable as regards the Torpedo for reasons which I shall give later (p. 446).

The animals employed belonged to the species *Torpedo marmorata:* they varied in length from 25–36 cm. The latter is the measurement of a medium sized European Torpedo.

2. General observations on experiments on Torpedos.

The transport of living Torpedos from Trieste to Berlin is not possible in all weathers. Frost is no less injurious than summer heat. Consequently the season for successful conveyance of the animals is limited to the months of April, May, September, and October.

The Physiological Institute in Berlin possesses its own fully-equipped Aquarium. However, I thought it better to take advantage of Dr. Hermes' kind offer to keep the Torpedos in the tanks of the Berlin Aquarium, which is only a few minutes distant. Here,

[1] Monatsberichte der Akademie, 1858, p. 94.

[2] See No. VI. of this work.

if they arrive in good condition and are kept quiet, they continue healthy for six weeks without material loss of vigour. Subsequently some animals died, which from want of leisure I had not been able to use for experiment, but others survived several months, although the temperature of the sea water was only 12° C[1]. According to the statement of the keeper, the Torpedos as long as they are in good health burrow in the gravel at the bottom of the tank and are then difficult to distinguish from the ground[2]. They do not trouble themselves about other fish in the tank. They were not seen to eat any of the fragments of fish which were thrown into it as food. In the free state Torpedos swallow, as Professor Fritsch ascertained by examining the contents of the stomach, very large fish which they previously paralyse by electrical shocks[3]. It is obviously, however, not easy to provide living small sea fish for them in captivity.

On the days of experiment the fish was transferred by means of a landing-net into a tub of such size that two men could carry it easily. And by the same means they were introduced into the experimental trough described below. The catching of the animal was accompanied by violent struggles, in which, no doubt, the fish gave repeated shocks, as was ascertained to be the case in the Gymnotus by connecting it with a rheoscopic limb of the frog[4]. I tried to obtain the same evidence here, but the rheoscopic limb remained motionless, no doubt in consequence of short circuiting by the sea water.

After the fish had been introduced into the experimental trough it remained quite quiet, the only motion visible being that of the spiracles. If it was put back into the trough after a long series of experiments, it swam wildly round and round, sometimes endeavouring by peculiar undulating movements of its body to get over the wall of the trough.

[1] Compare my observations as to the temperature at which pœkilothermal animals should be kept. Gesammelte Abhandlungen, vol. ii. pp. 605, 606, and in the Untersuchungen, p. 77.

[2] It was stated by Réaumur and Walsh that Torpedos at low tide burrow in the sand by working their pectoral fins, and that fishermen who step upon them with naked feet fall down (Untersuchungen, p. 132). Here a Torpedo incident told me by Ehrenberg may be mentioned, which gives an idea of the power of the Torpedos in the Red Sea (probably *T. panthera*). Ehrenberg had waded with his Arab servant on a coral reef deep into the water. Suddenly the man cried that a shark had bitten his foot off, staggered, and was on the point of falling down. With the quick perception of the naturalist, Ehrenberg reassured him with the words: 'Do not be afraid, there is no blood, you still have your foot, you have only trodden on a "Raâd."'

[3] Sitzungsberichte, 1883, vol. i. p. 205.

[4] Gesammelte Abhandlungen, pp. 615–617.

3. Method of leading-off Malapterurus shocks into an experimental circuit.

By the term experimental circuit I designate as before a circuit however arranged, whether continuous or otherwise, into which the shock is led for the purpose of testing any of its actions[1]. One of the first problems in the experiment is obviously to arrange this conduction as favourably as possible. When the animal is taken out of the water this is not difficult; but even when you have a living animal at your disposal, it is undesirable to risk its life for one observation; moreover, fish that have been taken out of water are usually so violent that it is disadvantageous to experiment with them. It is therefore necessary to obtain a solution of the problem which is applicable to animals which are still in the water.

Faraday in his researches on Gymnotus used for this purpose special arrangements. He applied to the fish two saddles of thin copper, covered externally with indiarubber. The further these saddles were apart from one another, the stronger was the derived current. If very strong actions were required, he placed glass plates on the bottom of the trough to which the indiarubber border of the saddle was so attached, that the part of the fish grasped by it was almost as completely insulated as if in the air[2]. Faraday does not appear to have thought of insulating the fish between the saddles, indeed, it would be hardly possible to apply a cover so as to enclose the whole of so long and wriggling a fish. In consequence of the great intensity of the Gymnotus shock Faraday's contrivance answered for almost all purposes, it was, however, difficult to obtain discharge shocks[3]. I was not able to recommend any better arrangement to Dr. Sachs for leading off the shocks. The saddle employed by him differed from that of Faraday in this respect, that instead of being made of copper coated externally with indiarubber, it was made of guttapercha lined with tin, after the model of the leading-off plates which I used for the Malapterurus. On the left side of the figure the lacquered strip of tin is shown which serves to connect the lining with the leading-off wire.

In working with the small and relatively weak Malapterurus, I found that the application of the saddles to the ends of the organ was insufficient, and that it was necessary also to insulate the fish between the saddles from the water. This was easily effected by

[1] Gesammelte Abhandlungen, vol. ii. p. 612. [2] *Loc. cit.* p. 5. nos. 1758–1760.
[3] *Loc. cit.* p. 7. no. 1767, note 2. Comp. Untersuchungen, p. 158.

means of leading-off plates made of guttapercha shaped like the covers of mummy coffins, and lined with tin at both ends; these are shown in Fig. 12; one was made for each fish according to a pattern cut to proper size. In using the cover a plate of glass was laid at the bottom of the experimental trough, this was filled to such a height that the surface of the water a, a' (for the sake of distinctness put too high in the figure) coincided with the back of the fish which rested on the glass plate. I observed that the insulation of the fish between the saddles more than doubled the shock in the experimental circuit. The insulation was so complete that when the electrodes of the frog-alarum were plunged into the trough at two diametrically

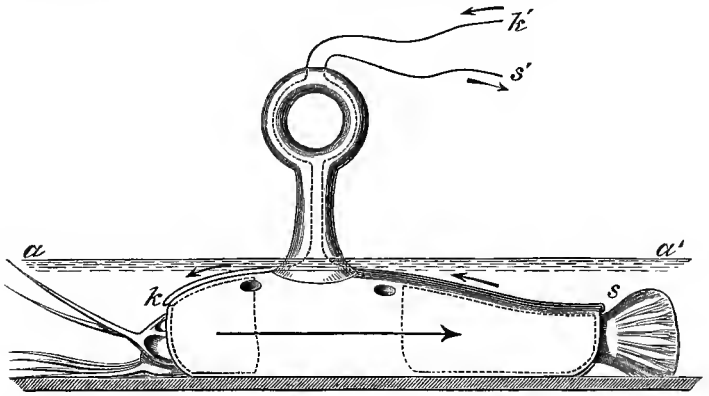


Fig. 12.

opposite points of its circumference no indication was obtained. It would have been still more perfect if I had closed the posterior opening of the cover with a cap arching over the caudal fin.

In contriving this cover the question arose what length should be given to the lining in order to obtain the strongest current in the experimental circuit. I found that it was advantageous to have a longer lining when the resistance of circuit was great, shorter when it was small [1]. I had expected this, and it will be seen from what follows that it must be so.

The connections k, k' and s, s' of the two linings may be regarded as terminals of the experimental circuit. According to Helmholtz's 'principle of the electromotive surface[2],' the strength of the current in the experimental circuit is equal to the difference of potential of the points of the lining which are in contact with its

[1] Gesammelte Abhandlungen, vol. ii. pp. 636, 637.

[2] Poggendorff's Annalen der Physik und Chemie, 1853, vol. lxxxix. p. 211.

ends, divided by the resistance of the circuit plus that of the organ, of the fish, and of the surrounding water, etc. between those points. The linings serve not merely to lead off from the ends of the electrical organs, but so far as they extend over their lateral surfaces, also constitute good conductors between these surfaces and the ends. As by this conduction part of the shock is short circuited, the difference of potential at the ends is the less the smaller the distance between the two linings. In other words the difference is the less the longer the linings. Further it is not quite independent of the position of the point at which the lining is connected with the circuit; for as the linings themselves conduct from the ends of the organs to the opposite borders, the potential varies in them in the same direction. Consequently the arrangement adopted on constructive grounds, according to which the ends of the circuit are respectively united to the anterior border of anterior lining, and posterior border of posterior lining is theoretically the most correct, although in practice the difference can scarcely tell.

The resistance of the organ, fish, etc. between the leading-off points of the two linings, is according to Helmholtz's law the same which the conducting mass would oppose to a current produced by an electromotive force acting in the experimental circuit. But in relation to such a current the linings constitute in accordance with known principles [1] isoelectric surfaces. Thus the resistance in question becomes larger the shorter the linings, smaller the longer the linings: inasmuch as their extent determines the area of the surface of application of the moist to the metallic conductor.

Let P_l and P_k be the differences of potential of the ends of the experimental circuit with a long and short lining respectively, and the corresponding resistance between the linings W and W_k; and further, let the great resistance in the experimental circuit be R, the small r, then, according to observation, we have the two following inequalities:

$$\frac{P_k}{W_k+R} > \frac{P_l}{W_l+R}, \qquad \frac{P_l}{W_l+r} > \frac{P_k}{W_k+r},$$

this involves the inequalities $P_k > P_l$, $R > r$, and as we have seen the latter to be proved, the observed relations are explained. The current flowing through the experimental circuit combines in every point of the conducting mass between the linings, with the current which would exist at the same point if there were no experimental

[1] G. S. Ohm, die galvanische Kette Mathematisch bearbeitet, Berlin, 1827, p. 128. G. Kirchoff in Poggendorff's Annalen der Physik und Chemie, 1843, p. 500.

circuit, according to the parallelopiped of forces [1]. For a complete theory it would be necessary to take into account induction and the manifold polarisations which exist, the main fact, however, would remain unaltered by these considerations.

4. Method of leading-off the Torpedo-shock into an experimental Circuit.

Difficulties are met with in the endeavour to carry out the same principles in leading-off the Torpedo-shock in the most satisfactory manner. The dorsal and ventral surface of each organ must have a metallic cover applied to it, and these covers must be led off from their median edges which, for reasons hereafter to be mentioned, are the most positive points on the back and the most negative points on the belly (see p. 430).

If the fish is in air nothing stands in the way of such a leading off; and Boll who simply fixed his Torpedo, used guttapercha plates lined with tinfoil after the pattern of my leading-off cover for Malapterurus, one of these plates being in as close contact as possible with the dorsal and the other with the ventral surface of the electrical organ [2]. But if the fish remains in the water it is no easy problem to apply the plates to the ventral surface of the organ; and it is still more difficult to insulate the rest of the fish at the same time, which is, however, especially desirable on account of the conductivity of sea water [3]. All this may be effected with such a fish provided that it is laid down in the experimental tub upon a guttapercha plate of greater extent than its body, the plate being provided with two metal shields corresponding to the organs, the median edges of these shields being in connection with one end of the experimental circuit. A guttapercha plate must at the same time be placed upon the back and moulded to its convex form. This plate must also bear two suitable shields applied and led off in the same manner. The root of the tail must be left free, but the two plates surrounding the body must be everywhere in connection with each other.

Unfortunately this plan theoretically so faultless is by no means convenient in practice. The fish refuses to lie on the lower plate

[1] See Helmholtz, *loc. cit.* p. 219. In the Gesammelte Abhandlungen, I gave an explanation of the different action of the long and short lining which I had less thoroughly thought out; in this the insufficiently determinate conception of a 'mean tension of the lining' was introduced. In place of this explanation the one given in the text must be taken.

[2] Reichert und du Bois-Reymond's Archiv für Anatomie und Physiologie, 1873, p. 78.

[3] Compare Arthur Christiani in the Untersuchungen, pp. 411 et seq.

as it ought to do, while the arrangement of the upper plate, on account of its extent, its double curvature and slight arching is very difficult. Besides which it bends in such a way that it is not easy to connect its warped undulating edge with that of the lower plate. Finally as it is not a question of experimenting as long as possible on a living subject (as was the case with my Malapterurus), an apparatus adapted only to a particular animal is not of great service. I therefore contented myself with the less rational but much simpler arrangement diagrammatically represented in Fig. 13, which was in point of fact sufficiently satisfactory. A glass

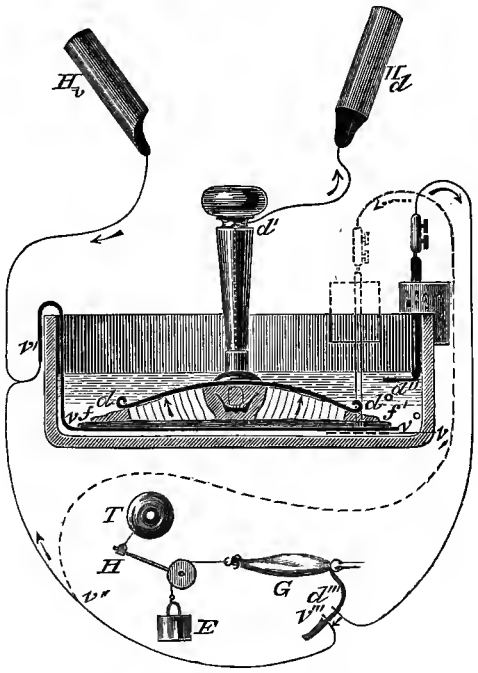


Fig. 13.

vessel 30 cm. wide and 10 cm. deep was used instead of the experimental tub. On the bottom of it rested a circular zinc plate of about the same width as the body, forming a ventral shield $v^\circ v$, a portion of which vv' was bent and hung hook-like over the side of the vessel. One end of the experimental circuit was brought into contact with this hook. The arrangement shown assumes that a shock will be imparted to the human body; accordingly there are two handles in the experimental circuit, to one of which Hv, the wire $v'H$ is conducted. A circular piece of flannel ff' was laid on

the ventral shield, soaked with sea water, to prevent the edge of the dorsal shield *d°d* from ever touching the ventral, the effect of which would be to render the result in the experimental circuit as useless as in Humboldt's and Gay Lussac's key experiment[1]. The fish rests on the flannel, and is represented in the figure as if in cross section through the organ. The dorsal shield is an arched zinc plate with the edge turned up, the upper surface of which is lackered, having a wooden knob in the middle through which the leading-off wire *d'Hd* is conducted insulated to the second handle. The diameter of the dorsal shield corresponding to the median plane of the fish is indicated by a red mark. I had two shields for Torpedos of different sizes, the one 22 and the other 18 cm. in diameter. The sea water in the vessel was in sufficient quantity for its surface just to touch the back of the fish.

5. Sluggishness of the Torpedo in confinement.

In the case of the Malapterurus the putting on of the shield was sufficient to induce them to give shocks, and if not fatigued they would give two or three in succession[2]; if the cover was pressed down upon them they would give more frequent shocks with convulsive movements until exhausted. The Torpedos on the contrary often failed to react when the dorsal shield was put upon them, and indeed there was no certain method of exciting them to give shocks when in this condition. They would allow themselves to be squeezed, rubbed, pricked, pinched either on the dorsal or ventral surface so far as these were accessible, without being excited to action. No shock was induced even when I applied the fully pushed up secondary induction coil connected with a Duchenne brush, to a portion of skin which projected out of the water, although at the same time the gastrocnemius of the frog-alarum was tetanized. As these Torpedos had not been nearly so long in captivity or kept without food as had been the case with the Malapterurus, it must be assumed that there is a difference in the nature of the two kinds of electrical fish. It would appear, however, from the statements of Walsh, Matteucci and Colladon as to the behaviour of their freshly-caught Torpedos[3], that this difference

[1] Gilbert's Annalen der Physik, 1806, vol. xxii. p. 8. Untersuchungen über thierische Elektricität, vol. ii. part i. pp. 15, 105. Gesammelte Abhandlungen, vol. ii. p. 695.

[2] Gesammelte Abhandlungen, vol. ii. p. 617.

[3] Untersuchungen, p. 255. Matteucci, Traité des Phénomènes électro-physiologiques des animaux, Paris, 1844, p. 145.

consists only in a more rapid loss of power by the Torpedos; and in fact Matteucci and Boll report that 'the energy of the electrical organs is rapidly diminished in captivity[1].'

The uncertainty whether in individual experiments the fish had been excited or not, made it most desirable to be assured on this point by means of the frog-alarum. Fig. 13 shows how I usually connected it with the fish. The diagram is easily understood—the Gastrocnemius *G*, the bell *T*, the hammer *H*, the weight *E*. The electrode *v'''* (not represented in the figure) of the exciting tubes was connected by the wire *v''v'* with the ventral shield. The other electrode *d'''* was connected by the wires *d'''*, *d''* with a circular zinc plate 3 cm. in diameter which extended horizontally from the edge of the basin under the sea water; it served for the frog-alarum the purpose of the dorsal shield. In experiments in which no ventral shield was used the ring electrode *v'''* was connected with a similar zinc plate *v'* (shown in the figure by a dotted line) on the floor of the basin. The frog-alarum did not seem to be so reliable as in the experiments on Malapterurus, a result which was partly due to the greater conductivity of sea water than of fresh. Moreover it frequently happened that Torpedos received in spring were more excitable, and, like the Melapterurus[2], according to the evidence of the frog-alarum, from unknown causes gave shocks of themselves.

6. Effect of Torpedo-shock on Man.

If the handles are grasped with wet hands, and the fish is effectually excited, a shock is felt which only affects the wrist, for reasons already set forth[3], but which gives a better idea of the phenomenon than any method of seizing the fish directly which can be devised. By this means I communicated the shock to a number of students at my lectures who joined their wet hands together. The weakness of the Torpedo-shock as compared with that of Malapterurus (still vividly present to my mind) was very striking. As, however, in my method of receiving the first shocks, the strength of the Torpedo-shocks is necessarily much diminished from the absence of insulation and the good conductivity of sea water, I cannot regard this observation as a confirmation of Babuchin's statement that the strength of the shock of Malapterurus exceeds

[1] Archiv für Anatomie, 1873, p. 78. Professor Fritsch complains of the sluggishness of Torpedos in winter, even when freshly caught in the Mediterranean. Sitzungsberichte, 1882, vol. i. p. 500.

[2] Gesammelte Abhandlungen, vol. ii. p. 408.

[3] Ibid. vol. ii. p. 619.

that of the Torpedo[1]. The influence of the good conductivity of the medium on the strength of the shock was clearly shown in Dr. Hermes' experiment with a Malapterurus, which every time that it was brought (for a curative purpose) into a physiological salt solution, just as in my observations on the gastrocnemius of the frog[2], apparently lost its electrical properties[3].

The late A. von Bezold, who helped me in my experiments on Malapterurus, suggested that the shocks might be strengthened by the substitution in the experimental vessel of aerated distilled water for river water[4]. As many fish ascend rivers from the sea (e. g. the Narcine Brasiliensis brought to Humboldt in Cumana as Tremblador or Gymnotus, was fished from the Manzanares[5]), it might presumably be possible without great risk to transfer a Torpedo for a time into fresh water. I would gladly have attempted to make observations on the strengthening of the shock which might be looked for under these circumstances, but on account of the sluggishness of the Torpedo it would have been fruitless to make comparative series of observations on the strength of the shock under varying conditions.

7. On the distribution of the current in the Torpedo.

The accompanying woodcut is a faithful reproduction of a figure by Cavendish, who, more than a century ago, in his endeavours to imitate by ordinary electricity the Torpedo-shock, first conceived the idea of current curves, and was so much in advance of his time in his understanding of this process in the animal, that Faraday was the first after him to attain to the same standpoint. Cavendish sought to accomplish his purpose by means of a leather model of the fish soaked with sea water; he covered the spots corresponding to the polar surfaces of the organ with tinfoil, and connected them by insulated wires with a Leyden battery[6]. By this means the polar surfaces became isoelectrical. Cavendish passed over in

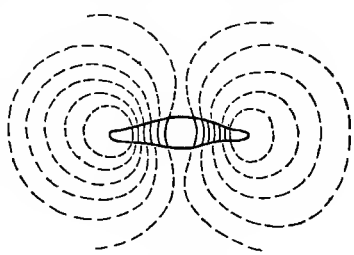


Fig. 14.

[1] Untersuchungen, p. 411.
[2] Gesammelte Abhandlungen, vol. ii. p. 379.
[3] Untersuchungen, pp. 409, 411.
[4] Gesammelte Abhandlungen, p. 613.
[5] Untersuchungen, pp. 76, 282, 411.
[6] The Electrical Researches of the Hon. Henry Cavendish, edited by J. Clerk Maxwell, Cambridge, 1879, p. 194.

silence the course of the current curves in the animal itself, nor could he form any distinct conception of them, for it was not until seventy years later that I showed that the assumption of the existence of insulating sheaths in electrical fishes was both superfluous and anatomically inadmissible[1]. We are now able to correct and complete Cavendish's diagram in both directions.

In 1831 Daniel Colladon of Geneva, by his investigations at La Rochelle, arrived at the three following propositions as to the distribution of electricity on the surface of the Torpedo when giving a shock.

1. All points on the back are positive to any point on the belly. The strength of the current diminishes in proportion to the distance of these points from the organ, and almost entirely disappears at the tail.

2. Any two unsymmetrical points of the back, or any two of the belly, almost always yield a current in the galvanometer. The one nearest to the organ is positive in the back, negative in the belly.

3. When contact is made with two symmetrical points either of the back or belly, there is no deflection in the galvanometer.

As Colladon was the first to determine the electrical condition of the dorsal and ventral surfaces of the Torpedo, I have given the name of Colladon's currents to the currents between points on either of these surfaces.

Colladon's observations were published in 1836. A year later Matteucci, who had previously denied the existence of such currents, asserted (without mentioning Colladon) that the points of the organ corresponding to the entrance of the nerves were positive on the back, negative on the belly; a statement which is connected with the erroneous opinion he then held as to the origin of the electricity in the brain of the Torpedo[2].

As I had already foreshadowed to myself the electrical plates since made known by Bilharz, I preferred another explanation[3]. The greater the length of a Torpedo column, provided that the number of plates in a unit of length is the same, so much the greater must be its electromotive force. The columns diminish in height from the inner to the outer edge of the organ by about 0·6

[1] Gesammelte Abhandlungen, vol. ii. p. 678.

[2] The literature, both old and new, of the subject is to be found in the Gesammelte Abhandlungen, vol. ii. pp. 684 ff. I may remark that the concluding sentence of par. vi. p. 690, is not quite exact as to Matteucci's frequently changing expressions, but the correction of it would require a lengthy setting forth and is no longer of interest to any one.

[3] Preliminary sketch of an investigation of the so-called frog-current and of electromotive fishes. Poggendorff's Annalen, 1843, vol. lviii. p. 25, par. 64, 65. Gesammelte Abhandlungen, vol. ii. pp. 668, 670. Untersuchungen, pp. 284, 285.

(see Fig. 15); by so much, therefore, may the electromotive force of the median columns be greater than that of the outer ones. This explains why when a Torpedo gives shocks in the air, a current is observed in the back from the median to the outside points, and on the belly in the reverse direction. In Torpedos under water this arrangement seems to be adapted to its purpose, inasmuch as the curves of currents proceeding from the higher columns have almost the same strength as the shorter ones which proceed from the lower columns.

As Matteucci gradually altered his opinions and allowed that the current flowed on the back from the thicker to the thinner parts, and also indicated the existence of a stronger current between back and belly in the thicker than in the thinner, so he later (without mentioning me) adopted the explanation given by me in the 'Preliminary Sketch.' I did not, however, adhere to this explanation, for I found later that it was not well founded. By an experiment in which I suddenly plunged into water zinc platinum elements grouped like electrical plates, I imitated, sufficiently for the purpose though very imperfectly, a shock given under water, and thus tested my conclusions regarding its distribution. These observations have already been given in detail, and I will here confine myself to recalling the results.

An arrangement of electrical plates which corresponds to a slice of the organ of the Torpedo bounded by two cross cuts, in which therefore the number of plates in the columns diminished from the one side to the other, yielded quite regular currents which were directed from the higher to the lower on the positive aspect of the organ, and from the lower to the higher on the negative[1]. It was found however experimentally, as on theoretical grounds might have been anticipated, that Colladon's currents occurred even when there was no difference in the height of the columns. If an electrical organ having columns of the same height were placed in an unlimited quantity of water, the middle districts of the polar surfaces would be relatively the most positive and the most negative. Let us suppose all the columns of the organs of the Torpedo to be of equal height, and the organs to be brought together in the middle plane and there united; then the middle of the median line would be most positive on the dorsal aspect, most negative on the ventral. Let the organs be again separated, then

[1] Comp. Untersuchungen über thierische Elektricität, vol. i. pp. 644 ff. Gesammelte Abhandlungen, vol. ii. p. 688.

the most positive and the most negative spots in each organ after the separation would assume a position intermediate between the median edge and the middle, which last would only be reached if the organs were placed at such an indefinite distance from each other that each could be regarded as alone existent.

Thus it is clear that even apart from the diminution in the height of the columns towards the sides, currents would exist on the back and belly of the Torpedo in the direction observed. The thinning of the organ towards the sides would nevertheless have the effect first of strengthening these currents, and secondly of shifting the points of greater and lesser positivity and negativity to the median borders of the organ. It would also appear that differences of tension due to inclination-currents similar to those observed by me in oblique sections of muscle, would act in the same direction[1]. Another conclusion may be drawn from all this which is especially important to me at the point at which I have arrived. The median borders of the organ being the most positive dorsally and the most negative ventrally, they must necessarily be relatively more positive and more negative than the middle line. So that there must be currents on the back from the borders towards this line, on the belly from the latter to the former. Colladon's second proposition and Matteucci's statement that the points of nerve entrance on the back and belly are relatively the most positive and the most negative (see p. 428), might appear to imply that the authors had actually observed the state of things indicated above. But it is unlikely that the means at their disposal were sufficient, or that they would not expressly have mentioned an observation so remarkable. However this may be, the result will show that it was worth while to put our conclusions on this matter to the test of experiment; and for many years I waited a suitable opportunity of doing so[2].

A Torpedo 29 cm. long was placed on its belly in a vessel filled with just enough sea water to cover the back of the animal. The following arrangement was used to lead off the shocks into the experimental circuit. Two amalgamated zinc plates, each 10 cms. long and 2·5 broad, enclosed in corks, could be placed in every position and at any desired distance in the manner described by Norremberg[3]. Oblong pads[4] of equal breadth with the plates were connected with them; they were soaked with sulphate of zinc

[1] Gesammelte Abhandlungen, vol. ii. pp. 93–127.
[2] *Loc. cit.* p. 690. [3] *Loc. cit.* p. 648. [4] *Loc. cit.* vol. i. p. 7.

solution. To these others were attached similarly soaked with sea water. These last were pointed, and the points projected beyond the zinc pads so as to touch the surface of the fish at the spot at which it was to be led off. The zinc plates were connected by wires with the galvanometer, the bobbins of which possessed 5000 turns, at a distance of 30 mm. from the very light reflecting magnet which was quite aperiodic[1]. If the fish gave no shock the mirror was deflected only a very few degrees of the scale. These inequalities were balanced by the round compensator. The frog-alarum was brought into connection with two horizontal zinc plates, one of which rested on the bottom of the glass vessel, while the other just dipped into the water (see above, p. 426). I observed the galvanometer, Prof. Fritsch who is accustomed to handle Torpedos manipulated the fish, and Prof. Christiani took charge of the rest of the arrangements.

When one point was placed upon the median and the other upon the outer edge of one organ, in a line which bisected it about equally, and the fish was excited, a deflection was observed almost simultaneously with the sound of the frog-alarum, and this deflection (through the galvanometer) was always from the median to the outer edge. The extent of the deflection was very unequal, e.g. on one day it was 135 right and 100 left, while on another it was 100 right and $500+x$ sc. left; that is to say, in the latter case the scale disappeared from the field of vision. These differences may have in part arisen from differences of resistance in the circuit caused by the greater or less pressure of the pointed pads; for the most part, however, they depended on the irregular efforts of the fish. When deflections were observed beyond the limits of the scale it is possible that several shocks occurred in such rapid succession that they were confused in the frog-alarum.

If one point was placed upon the median edge while the other was placed upon the median line, deflections occurred constantly in the direction previously observed, namely from the edge of the organ to the median line. Thus in four cases the amount of deflection was

	Right.	*Left.*
1	30	
2		15
3	20	
4		19 sc.

shewing as much regularity as could have been anticipated. The

[1] I used Mirror I of my first Treatise 'Ueber aperiodische Bewegung gedämpfter Magnete.' *Loc. cit.* vol. i. pp. 308, 309.

fish was then laid on its back. The frog-alarum showed that the violent efforts of the fish to turn over again were accompanied by numerous shocks. In this case the points were on the one side upon the median line, on the other upon the median border of the organ corresponding to the gill openings, and the results of the shock were 160 right sc. and 70 left sc. in the expected direction, that is, from the median line to the border of the organ.

A shock between the back and belly always shot the scale far out of sight, and in the first experiments, when so many points of great importance pressed for observation, no comparison was made of the strength of Colladon's currents with that of the shock between the polar surfaces.

On the other hand, in order to be perfectly sure of the existence of the new currents, I did not fail frequently to lead off the shock from symmetrical points. I had, however, a different result from that put forward in Colladon's third proposition (see p. 428), namely, that in continuation of the last experiments there occurred between two points on the ventral surface outwards from the nasal openings a deflection of 160 sc. from right to left; on another day between corresponding points on the dorsal surface a deflection of 42 sc. from left to right, and between two symmetrical points of the body some centims. behind the organs, 29 sc. in the same direction. When I allowed the left point to stay where it was, and placed the other on the posterior edge of the left pectoral fin, a deflection of 230 sc. was seen in the expected direction, that is to say, from the point nearest the organ towards the more distant one.

The results observed between symmetrical points show nothing more than that the fish does not give a shock of equal strength with both organs. In both experiments on the ventral surface, as well as one on a later day on the dorsal surface, it usually gave a stronger shock with the left organ. The reason why similar results were not seen by Colladon may perhaps have been that his very strong fishes innervated both organs equally. Perhaps also these results were beyond the reach of the means of observation at his disposal, for in this case the new currents observed by us between the middle line and the median border of the organs must necessarily have escaped his notice.

The importance of the last named currents consists in what follows. De Sanctis objected to my doctrine of the relative immunity of electrical fish from their own shocks, that he experienced no shock when his hand was inside the body of a Torpedo which

was out of the water. He concluded from this circumstance that only an inconsiderable portion of the shock goes through the body of the fish, without taking into account that this might be the case with a fish exposed to the air but need not be so with one under water. In the air, the current in order to go through the body must take its way along the thin, perhaps half dry, skin, and it is not therefore surprising that a hand inside the body should feel very little of it[1]. Meanwhile even under these circumstances Boll succeeded with the Torpedo, following my procedure with Malapterurus, in detecting the shock in the interior of the body of the fish by means of wires insulated to the points[2].

The proof that the Torpedo-shock really penetrates the body of the fish and attains a greater density than elsewhere in the brain and spinal cord, and in the great nerve trunks, is not thereby weakened. The currents, which in the back flow from the median borders of the organ to the middle line, and in the belly from the middle line to those borders, necessarily take their course through the brain and spinal cord, and as this is the shortest path between the most active portions of both organs, there exist no stronger currents in the Torpedo. As in Malapterurus so here my assertion is confirmed, that the body of the electric fish itself is more favourably placed for receiving the shocks of its own organs than that of another creature in its neighbourhood[3].

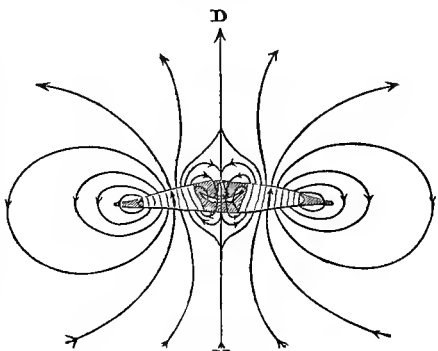


Fig. 15.

A glance at Fig. 15 makes this clearer, and also shows how in consideration of the results we had obtained we needed to alter Cavendish's diagram. The cross section represented, including the columns which are only diagrammatically indicated, is drawn strictly from nature. The first fact to notice is that the current

[1] Compare Untersuchungen, p. 128.

[2] *Loc. cit.* pp. 260, 261.

[3] Monatsberichte der Akademie, 1858, p. 107. Gesammelte Abhandlungen, vol. ii. p. 638.

curves do not merely stream out from the so-called polar surfaces, but also cut the lateral surfaces of the organ[1]. They then run inward and outward through the body of the fish and occupy the surrounding space. The curves do not, however, as represented by Cavendish, start from the polar surfaces of the columns as prolongations of their axes. But the curves in this direction, according to the principle of the superposition of currents, blend with the curves which tend from the thicker to the thinner portions of the organ and through the latter to the ventral surface. Hence it arises that the resulting curves are inclined towards the sides as shown in the figure. A circumstance occurs here with which I had previously to deal in my 'Experimental criticism of the discharge hypothesis.' A nerve end-plate, regarded as an electrical plate, which therefore has a stronger electromotive force the thicker it is, and which becomes thinner from the middle towards the edge, resembles the Torpedo organ, which in like manner decreases towards the sides. Here, therefore, if there are really nerve end-plates in this sense, the curves of the current must stream obliquely out of the one surface and into the other[2]. If you imagine a sagittal section through a Torpedo organ, there being from front to back no diminution in the height of the columns comparable with that in the transverse direction, the direction of the curves in the sagittal plane would be primarily that of the columns. The whole system of curves could only be made clear by means of a model.

The inclination outwards of the median columns shown in the figure (their electromotive action being parallel to their axes) must influence the direction of the current curves on the back in the same way as the greater height of the median columns, whereas on the belly, as indicated in the figure, the inclination of the curves is lessened by the same circumstance. The oblique position of the columns is more strikingly seen in the drawing of the cross section of a young Torpedo given by Fritsch in the Memoir alluded to on p. 419. By this means the region over the middle of the fish is apparently deprived of denser current curves and, to use a military expression, becomes comparable to a dead angle (zu einem todten Winkel). The teleological signification of this arrangement is obscure, for when the fish, in its favourite position, lies half buried at the bottom of the sea, the dorsal surface seems to require the greatest protection, while the ventral surface is not in need of any.

[1] Gesammelte Abhandlungen, vol. ii. pp. 629, 682. Untersuchungen, p. 148.
[2] Ibid. vol. ii. p. 708, Fig. 47.

8. On Iodide of Potassium Electrolysis by the Torpedo-shock.

When, following Faraday's procedure with the Gymnotus, I made use of iodide of potassium electrolysis in order thereby to determine the direction of the shock in Malapterurus, I came upon the phenomenon of the secondary iodine spot (as already many times related); that is to say, I saw a spot arise under the negative as well as under the positive platinum point. I at once perceived that I had before me an occurrence with which I had already become acquainted when I employed the same means for ascertaining the direction of the current in complicated induction-circuits[1]. The platinum points are polarised by the decomposition of the iodide of potassium, and if the circuit is not instantly opened again, whether in experiments with the induction coil or with electrical fish, a secondary or polarisation-current follows on the top of the primary-current in the opposite direction, and gives rise to a spot on the formerly negative but now positive point. I was induced by the experience of the Malapterurus experiments to make the appearance of the secondary iodine spot the object of a complete investigation, of the results of which I will recall only one or two. In the first place, if the quantity of electricity in the primary-current which is restored within the unit of time exceeds a certain limit no secondary spot is seen. But there are circumstances in which the secondary spot surpasses the primary, so that the iodide of potassium electrolysis becomes a completely deceptive indication of the original direction of the current. This is the case if, besides the platinum points dipped in iodide of potassium solution, another pair of platinum electrodes in say a weak solution of sulphuric acid, are also in the circuit[2].

The possibility of the double iodine spot being caused by a double shock of the fish was worth considering. I satisfied myself by means of the frog-interrupter that this was not the case. The secondary spot was absent if the circuit was opened either immediately after the shock or towards the end of it. Besides this, in Malapterurus it was sometimes possible to make the secondary spot the stronger of the two by leading-off from the fish with platinum electrodes. Thus the dependence of the secondary spot on polarisation was established in this case, and in this respect there remained no obscurity as regards Malapterurus.

It is, however, incomprehensible that none of the observers who

[1] Untersuchungen, vol. ii. Part i. 1849, p. 400.
[2] Gesammelte Abhandlungen, vol. ii. pp. 648, 666.

before me undertook so many times iodide of potassium electrolysis, both with Gymnotus and Torpedo, should have mentioned the secondary spot—not even Faraday, who made use of this means for the purpose of studying in the fish the distribution of tensions. Perhaps in Gymnotus the shock is too strong to allow the formation of the secondary spot. Even Sachs, on whom I pressed the clearing up of this point, failed to obtain the secondary spot in Gymnotus[1].

I was extremely curious to see what the result would be of my experiments on Torpedo. Nothing being needed for the experiment except the iodide of potassium electrolyser and the frog-alarum, I was able, through the kindness of Dr. Hermes, to undertake it as early as the summer of 1881 in the Berlin Aquarium (see p. 418). Since then I have often repeated it, and without exception have always seen the secondary spot, very black and at the moment of its appearance sharply defined, and I have also shown it to several other observers. In the first instance the electrodes applied to the fish were merely a couple of zinc plates, but afterwards the dorsal and ventral shields above described were used. It need not be said that care was taken that they should be homogeneous. The spots only appeared at the moment when the frog-alarum struck. Both spots seemed to me to be fainter than in the case of Malapterurus. I endeavoured by the use of platinum electrodes to make the secondary spot the larger of the two. In this I was not successful, although the spot was brought more distinctly into view. It was, however, easy to hinder the formation of the secondary spot by means of the frog-interrupter. An overweighting of 30 grammes delayed the opening of the circuit sufficiently to permit the formation of a primary spot, which was not appreciably smaller, without any secondary one. If the frog-interrupter was partly short circuited the secondary spot reappeared with the next shock.

Thus as regards the matter in hand all is clear with regard to the Torpedo, and the only obscurity which remains is why the secondary spot escaped the observation of all earlier observers, and especially of Matteucci, who led off with platinum electrodes as well as with platinum points, by which means the secondary spot is certainly strengthened if not always made the stronger of the two. I cannot imagine that the Torpedo-shocks by which John Davy and Matteucci decomposed iodide of potassium, exceeded in strength the powerful shocks of my Malapterurus to such an extent that the secondary spot did not appear in consequence of the larger quantity

[1] Untersuchungen, p. 163.

of electricity which was lost by derivation (see p. 435). The only other possibility already considered by me in the conclusion of my paper 'On Iodide of Potassium Electrolysis,' namely, that in those experiments in which the Torpedos were observed out of the water, the resistance of the circuit in which the polarisation discharged itself was too great, seems equally improbable considering the sensitiveness of the iodide of potassium. The fish was kept wet with well conducting sea water, the path of the current through it was short and of large section, and its tissues probably conducted better than those of Malapterurus; so that the resistance could scarcely be greater than in my experiments on the last mentioned fish[1]. Under these circumstances I cannot avoid the suspicion that the secondary spot must have been seen, but was passed over as an incomprehensible disturbance. Some indication of this appears in Matteucci's paper[2].

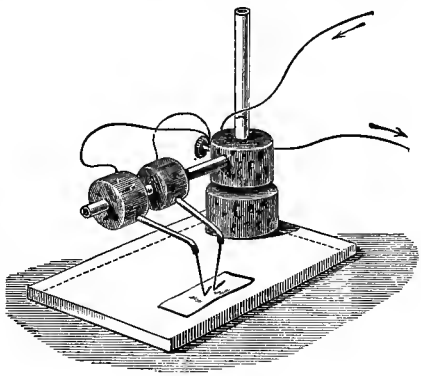


Fig. 16.

In order to put others in a position to repeat my observations in a similar manner, I represent in Fig. 16 the iodide of potassium electrolyser long used by me, and which in my opinion is an indispensable apparatus for the electrical laboratory, but is seldom met with, although very easy to construct.

[1] According to Leon Fredericq the blood of Octopus vulgaris and Astacus marinus contains nearly four times as much salt as that of mammals; and according to Boll the tissues of Torpedos have a 'physiological' concentration of 2·5 per cent. solution of chloride of sodium (Untersuchungen, p. 133). Perhaps on this account the tissues of marine animals conduct better. I have not yet found time to decide this point as regards Torpedos. Any other marine fish out of the Aquarium would be equally useful for the purpose. In accordance with Boll's statement the clay used in the Torpedo experiments should have been kneaded with a 2·5 per cent. solution, instead of the usual 0·75. I observed nothing, however, which could be regarded as an unfavourable result of this neglect. A superiority of sea fish over fresh water fish with respect to the ash of their muscles cannot with certainty be deduced from the 118 analyses of the flesh of fishes made by Atwater of Middletown, Conn., U. S. A., and published in the Berichte der deutschen chemischen Gesellschaft (vol. xvi. nos. 12, 23, July 1883). The summary of Koenig, however, seems to favour the notion (Die menschlichen Nahrungs- und Genuss- mittel, Berlin, 1883, 2nd ed. pp. 179, 180). According to Weyl the Torpedo organ yields 1·55 per cent. of ash, a quantity rather greater than that of the muscles of river fish in these determinations (Monatsberichte der Akademie, 1881, p. 382).

[2] Gesammelte Abhandlungen, vol. ii. p. 650.

The description will be found in the Introduction to the Treatise 'Ueber Iodkalium Elektrolyse.' It need only be mentioned here that the sheet of plate-glass measures 150 mm. long and 75 mm. broad, that the upright glass tube is 150 mm. in height, the horizontal axis bearing the corks measured from the axis of the upright tube is 125 mm. in length. As I have elsewhere remarked, the secondary spot is best observed when it is seen by inclining a glass plate placed at a suitable angle to the horizon, and looking at it from behind. In order that the iodide of potassium paper may allow the spot to shine through it, a single layer of the finest blotting-paper must be used.

9. Of the Organ-current in the Torpedo.

By organ-current I mean, in contradistinction to the shock, a current persistently generated through the organ and as a rule in the direction of the shock. Its electromotive force will be referred to as that of the organ-current. This action of the organ which reminds one of muscle tone, was first observed in the Torpedo by Zantedeschi, confirmed afterwards by Matteucci and denied by Eckhard. I overlooked it in Malapterurus. On the other hand Robin observed it even in the imperfect electrical organ of the Skate, and Sachs found it constantly in the Gymnotus[1].

I made a point of determining, if possible, the question as to the existence of an organ-current in the Torpedo. The Torpedo used in my first experiments of this kind was 36 cm. in length, and had been living in the Berlin Aquarium for about five weeks from the end of May. That it might be as little as possible exhausted by shocks before the experiment it was killed in the following manner. A sharpened borer prepared from a steel-tube 13 mm. in diameter, was placed by Prof. Fritsch on that part of the bony skull of the fish (which was lying tranquilly in the tub) which he knew corresponded with the electrical convolution of the brain. He punched out this convolution by a single stroke of the hammer, which drove the borer through the thickness of the fish into the

[1] Gesammelte Abhandlungen, vol. ii. pp. 672, 718, 722, 723. Untersuchungen, p. 169. As I recently discovered, Galvani in his fifth letter to Spallanzi ascribes to the Torpedo a persistent electrical action, which manifested itself in the twitchings of frog preparations, the feet of which he had applied to the fish. In one instance the frog preparation was suspended by a silk thread. Memorie sulla elletricità animale ... al celebre Abbate Lazzaro Spallanzani, Bologna, 1797, iv. p. 75. It must be remarked, however, that Galvani's statements are in some respects incomprehensible, and in others admit of a different explanation.

bottom of the tub. As a proof of the success of the operation the convolution adhered to the borer. The fish twitched a good deal but gave no shocks. It was taken out of the water and suspended with its body in a vertical plane by means of an anatomical hook thrust through the edge of the pectoral fin. Thus both the ventral and dorsal surfaces could be conveniently reached by the pads described on p. 430 placed horizontally. They were constantly so placed that the axes of the two coincided. The galvanometer had the same sensitiveness as in the experiments on Colladon's currents.

A current showed itself with the greatest regularity in the direction of the shock. It was strongest when the highest columns on the median edge of the organ were between the pads, and became weaker in proportion as the pads approached the thinner outer edge of the organ; e. g. if in the first case the result was 18 sc. it sank in the middle of the organ to 9 and at the edge to 3 sc. It was even traceable in the same direction in the median plane between the two organs, and at the edge of the body where no organ exists. This is quite in order, for the persistent current equalizes itself just as the momentary shock does in the skin and body of the fish, by branch currents which follow every channel that offers itself. In other words, if we put out of account the smallness of the differences of potential, the electromotive surface of the non shock giving fish differs probably from that of the same fish when giving a shock only in the induction which accompanies the shock. The results observed had nothing to do with the wound caused by punching out the electrical convolutions.

There was still another way of investigating the organ-current. In anticipation of experiments on Torpedos I had occupied myself for a long period in considering how a bundle of columns of regular limits could be so obtained as to serve for experiments such as those on muscle or on the organ of Malapterurus. This last is by nature so limited by the outer skin and inner tendinous membrane that it is easy with scissors to cut regular strips of a given length and breadth, whereas in dead Torpedos, which I had once received from Trieste, the prisms of the organs broke up into hour-glass form[1]. I had thought of all sorts of contrivances for encountering this difficulty, such as a revolving sharp borer like a trephine, with which cylindrical bits of the organ might be cut out, troughs of glass or ebonite, with removable sides, in which the bits could be confined. When at length, last summer, I found myself in presence

[1] Gesammelte Abhandlungen, vol. ii. p. 721.

of the reality, I discovered that all these preparations were superfluous. With a long, broad, straight knife, such as a ham-knife or an English bread-knife, the use of which on the Torpedo I learned from Prof. Fritsch, a strip 5–6 mm. thick can be cut from the organ. This includes only a few columns, and if the cut-surface is applied to strong cardboard it adheres firmly to it. From such a strip, four-sided prismatic bits of the organ can be cut with long-bladed paper scissors which are not too sharp. These four-sided prisms, limited by a bit of skin on the back and belly 5 or 6 mm. square, contain a considerable number of columns. Such a portion is placed upon the well-known three-cornered glass plate of the 'Carrier[1],' the bottom layers of skin are connected with the clay shields of the conducting pads to which they adhere; the pads are gently separated so as to draw out the columns to their full length. Such a preparation presents a very clean and neat object of investigation, the length of which naturally depends on the size of the fish and the part of the organ from which it was taken. The longest columns which I manipulated were about 29 mm. in length, and were therefore shorter than the group of muscles from the thigh of the frog. The bundles of columns appeared somewhat thicker.

My first idea was that the cut surfaces of the preparation would pass through the columns parallel to their axes, not between them, so that the lateral surfaces would be beset by shreds of electrical plates which would either stick to them or to each other, or roll themselves up. But the most careful examination with a lens in fluid failed to discover any such shreds. On the contrary the columns separate themselves from one another under the blades of the scissors with the fibrous sheath undestroyed. It of course sometimes happens that only the upper, under, or middle part of a particular column is attached to the bundle, but these irregularities can easily be got rid of. The shreds of plates if they existed would have no noteworthy electromotive action, or if they had, would retain it only for a very short time, so that they would only come into account as affording channels of derivation.

Such bundles of columns will be used for our experiments on polarisation, which I need hardly say are our most important problems. These experiments take the following form; as the

[1] Untersuchungen, vol. i. 1848, pp. 495, 496. [Professor du Bois' 'allgemeine Träger' is an instrument by means of which a preparation may be supported in the moist chamber in any desired position. Tr.]

bundles of columns do not twitch like muscle, it is not necessary to immobilize them. It is sufficient to make the conducting troughs, between the clay shields of which the bundle of columns rests on the triangular glass plate, the terminals of the polarising circuit, in order to lead the current in the manner best adapted to the purpose through the ventral and dorsal surfaces to the columns. A couple of non-polarisable conducting tubes serve for the purpose of leading-off the polarisation-current, the clay points of these are in contact with the preparation between the clay shields by which the polarising-current is led in.

The organ-current then showed itself quite regularly in the galvanometer-circuit just as Matteucci states that he observed it in cubical bits of the organ only 2 mm. wide [1]. This method of observation has the advantage that there can be no suspicion of any electromotive difference between the pigmented skin of the back and the unpigmented skin of the belly. In preparations of tolerably fresh organs the organ-current was always in the direction of the shock. It was easy to demonstrate that a column-like arrangement of the electromotive forces gave rise to it, for it appeared in the same direction no matter where the clay points were applied, and its strength increased with their distance from each other. For example, between the middle and a point of the lateral surface as near as possible to the dorsal end, it amounted to +13·5 sc. (The plus sign means that the effect took place in the direction of the shock.) Between the middle and a point nearest the ventral end, the amount was +10 sc.; but between the two outermost points +23 sc. That is, owing to the considerable resistance of the conducting tubes, only a little less than the sum of the effects of both halves. In another case the corresponding numbers were +5, +4, +11 sc. If the connecting line of the clay points cut the axis of the columns vertically no regular effect ensued worthy of being taken into account.

In these experiments I frequently measured the force of the organ-current and found it to be between 0·005 and 0·013 Raoult, considerably less therefore than the force of the nerve-current in frogs. The current force in bits about 4 cm. long of the organ of Gymnotus, were estimated by Sachs to be from 0·015 to 0·030 Daniell, the mean therefore being 0·0225. The length of my bundles of columns varied from 29 to 12 mm. according as they

[1] Archives des Sciences physiques et naturelles. Nouvelle Période, vol. xv. 1862, pp. 41, 42.

were taken from the middle or the outer edge of the organ in larger or smaller fish, their average length therefore amounted to 2 cm., and their average force was $\frac{0{\cdot}005+0{\cdot}013}{2}=0{\cdot}009$ Raoult, or about 0·0085 Daniell[1]. Double this length the force would have been 0·0170, and thus only a little less than the average force of much larger bits of the organ of Gymnotus.

This correspondence may indeed be followed still further. If one reckons an average of ten plates to a millim. in the Gymnotus organ, the medium organ-current force of the individual Gymnotus plates will be $\frac{0{\cdot}0000375+0{\cdot}0000750}{2}=0{\cdot}00005625$. On account of a correction which is probably necessary to be made in all Sachs' figures this value is raised to 0·00006. If in the Torpedo the medium number of plates to the mm. is reckoned to be 30 this gives 615 as the number of plates to the columns of medium height, that is $\frac{29+12}{2}=20{\cdot}5$ mm., but only 500 of these would lie between the conducting clay points. If we divide the average organ-current force observed by us, viz. 0·0085 Daniell, by this number, we have 0·0000117 Daniell, as the mean electromotive force of a single Torpedo plate. This value is 3·3 times less than that found for a single plate of Gymnotus. According to my ideas it ought to be about 8·5 times less on account of the thickness of the Gymnotus plates being about 8·5 times greater[2].

A closer coincidence between two numbers obtained under such circumstances is not to be expected. It is sufficiently surprising to find that the numbers are in similar order. Possibly it may be only a result of coincidence. Yet it may be regarded as a rare coincidence that from the same assumptions as those on which the above calculation is founded, I should arrive at the remarkable conclusion according to which the electromotive force of the whole Gymnotus bears to that of the whole Torpedo (in adaptation to the conditions of each), almost the same relation as, according to Christiani's determination, the resistance of fresh water to sea water[3].

[1] Compare E. Kittler, 'Die elektromotorische Kraft des Daniell' schen Elements.' Sitz. der math. phys. Classe der k. b. Akad. der Wissensch. zu München, vol. xii. 1882, pp. 501, 502. Also Wiedemann's Annalen der Physik und Chemie. N.F., 1882, vol. xvii. p. 893.

[2] Untersuchungen, pp. 174, 175, 278–280, 286.

[3] Ibid. pp. 414, 415.

For the present we may conclude that the electromotive elements are nearly of equal force in the two fish, and that the difference of potential of the electrical plates increases with their thickness. As regards Matteucci's statement that the force of the organ-current of the whole Torpedo lies between that of a single gastrocnemius of the frog and that of two such, it is sufficient to say that the electromotive force of the uninjured gastrocnemius is, through parelectronomy either nil or even negative, so that it cannot serve as a unit of measurement.

The force of the organ-current diminishes as the organ dies; it possesses, however, great tenacity of life[1]. In fish kept in the cold, an organ-current force of 0·003 to 0·002 Raoult is met with after 24 or even 48 hours. The persistence of the organ-current is a sign of the maintenance of functional activity. Later than this the preparations are not only inactive but occasionally the action is reversed, an observation already made by Zantedeschi as regards the whole fish[2]. Sachs made the same observation on Gymnotus though under somewhat suspicious circumstances[3]. One might seek to explain this reversed action after the cessation of the organ-current, by slight irregularities of a different kind, which according to their direction sometimes assume the semblance of remnants of normal organ-current, sometimes of a reversed organ-current. But this reversal of the current seems to occur too regularly to be so explained, and it recalls too distinctly the similar phenomenon which takes place, also with great regularity, in certain more delicate muscles as they gradually die[4].

The same diminution and irregularity in the force of the organ-current which is observed in the dying organ of Torpedo, appears to occur in the living fish under unfavourable circumstances as regards nourishment. For when I repeated the experiments in winter on a Torpedo 29 cm. in length which had been about seven weeks in the Aquarium and was killed as before by punching the electrical convolutions, I did not obtain the same effects, but only deflections indefinite in direction and extent, which might have been dependent on slight differences in the skin or on other disturbances. Even the bundles of columns from this fish were either inactive or showed reversed action, though one of them

[1] Berichte, 1882, vol. i. p. 500. Compare Untersuchungen, p. 188.
[2] Comptes rendus, 1842, vol. xiv. p. 489.
[3] Untersuchungen, p. 258.
[4] Ibid. vol. ii. pt. i. pp. 154, 283, 553.

manifested a good strong organ-current. In another Torpedo 26 cm. in length which had been even longer in captivity, and in which I did not experiment on the organ-current of the whole fish, I found the bundles of columns to act very regularly, and in some instances with considerable force.

The diminution of force of the organ-current in badly nourished animals would explain the fact that I found none in strips of the Malapterurus organ even with the nerve-multiplier. As regards what Eckhard considered his negative results, it will be seen on closer examination that they are not altogether inconsistent with ours. Of his experiments on the whole fish, of which to prevent voluntary discharges and movements the brain and spinal cord were destroyed, Eckhard remarks, 'The needle was seldom completely at rest but the deflections were always very small, and frequently at all events corresponded in direction to such a current as would be induced in the organ by the excitation of its nerves. There was, however, no permanent deflection.' Of experiments on bits of an organ led off from the ventral and dorsal surfaces he says, 'The deflections had often the same direction as above noted; they were not, however, to be compared with those resulting from much smaller portions of muscle of the same animal.' The organs and parts of organs gave shocks on excitation of their electrical nerves[1]. What this amounts to is simply that Eckhard expected stronger currents than those he actually observed, a circumstance which was due to the defective sensibility of his galvanometric apparatus. The absence of permanent deflections is explicable by the circumstance that Eckhard still used platinum for leading-off.

In the bundles of columns taken from the median part of the organ, it sometimes happens that nerve branches protrude from the middle of their length, as out of the tubes of a muscle. If a bit of nerve is cut off from the preparation a shock follows which may even drive the scale out of sight. Matteucci described a similar effect, having observed twitchings in a nerve muscle preparation in contact with bits of organ only as big as pin heads, when these were mechanically excited[2]. I tried in vain, however, to excite the bundles of columns with ammonia, although Sachs had succeeded in doing so with portions of the organ of Gymnotus[3]. The reason is clear, viz. that in bits of the Torpedo organ it would only be

[1] Beiträge zur Anat. und Physiol., vol. i. pp. 159–162.
[2] Untersuchungen, pp. 175, 176. [3] Ibid. pp. 177, 178.

possible to excite effectually, in the manner above related, a single column cut longitudinally.

In such preparations the organ-current often gradually diminishes. Matteucci in Torpedos, and Robin in the Skate observed it to rise somewhat after each shock, and something similar was also seen by Sachs in his observations on Gymnotus[1]. In the few experiments in which I succeeded in exciting bundles of columns by mechanically exciting the nerves, the rapid subsidence of deflection due to the shock blended itself in such a way with the effect of the organ-current, that the shock deflection presented itself as a mere transitory increase of the latter. But Sachs has further shown in Gymnotus that tetanus of the organ weakens the current[2]. I had no opportunity of making similar observations on the Torpedo.

10. On the secondary Electromotive Actions of the Organ of the Torpedo.

I started upon this virgin soil with the greater zest because, as the reader will remember, there seemed to be a contradiction between the results of my experiments on this subject on Malapterurus and those of Sachs on the Gymnotus. I longed to decide which of these two antagonistic observations would accord with those about to be made on the Torpedo.

The apparatus and methods of experiment which I used were the same that served for my recent researches on secondary electromotive phenomena in muscle and nerve. The manner in which the preparations of the organ were exposed to the polarising-currents, and in which the secondary-currents were led off has been already described. At the first glance it appears to be an advantage that the organ preparations do not twitch like muscle. On the other hand, as in nerve experiments, one is deprived of the evidence of the continuance of functional activity which the twitch gives in muscle. Although some of the difficulties which I anticipated did not appear, yet the preparations made in the manner described could not be compared in regularity with such naturally formed objects of experiment as we possess in nerves and in certain muscles. Whereas it is not difficult to provide for comparison a bit of sciatic nerve or a muscle of equal size and freshness, and uninjured, it is impossible to be assured of an equal number of uninjured columns in our preparation. In the same fish the length varies between the

[1] Untersuchungen, pp. 170, 173.

[2] Ibid. pp. 174, 187, 220.

median and outer edges of the organ; the functional activity of preparations cut from the same organ at short intervals of time is for unknown reasons very different; and in addition to this there is the variable amount of short circuiting caused by the remnants of cut columns which remain attached to the uninjured ones (see p. 440). These are the reasons (indicated on p. 418) why even that small degree of exactitude with which I was obliged to content myself in muscles and nerves, cannot be attained in polarisation experiments on the Torpedo columns themselves. A table of the secondary electromotive effects of the electrical organ similar to the ones which I drew up for muscle and nerve, with double entry, in which one head should comprise increasing current densities with currents in both directions, another head increasing closing times, could only be thoroughly carried out by someone who, like Boll at Viareggio, has at his disposal for weeks together at least five freshly caught fish daily, and who has no other object in view[1].

In what follows the secondary electromotive effects will be especially dealt with, which the current induces either in the direction of the Torpedo-shock or in the opposite direction. The former, according to the nomenclature employed by me in my book on Gymnotus, I call absolutely positive, the latter absolutely negative[2]. Polarisation in the direction from belly to back is therefore absolutely positive; and according as it follows an absolutely positive or negative polarising-current it may be considered relatively positive or negative. For the sake of greater facility in distinguishing polarising-currents with respect to their direction, I will call the current in the direction of the shock the HOMODROMOUS, and that in the opposite direction the HETERODROMOUS[3]. The homodromous current is indicated by an ascending arrow (↑), the heterodromous by a descending one (↓). Plus and minus signs serve to distinguish between relatively positive and negative polarisation. By 'both currents,' I understand simply the homodromous and heterodromous currents. Finally for brevity, it is desirable to call the polarisation whether through the homodromous or the heterodromous current, whatever its absolute direction may be, as relatively homodromous and heterodromous polarisation.

[1] Archiv für Anat. und Physiol., 1873, p. 77. [2] *Loc. cit.* pp. 149, 213.

[3] A colleague learned in philology whom I consulted with regard to these expressions, advised the use of 'isodromous' and 'anisodromous.' I considered, however, the forms introduced into the text more practical on account of the similarity of sound of the others to 'isotropous' and 'anisotropous' which are used in the description of the organ.

The first result of these experiments is that internal polarisation of the organ follows the passing of a current through it in the direction of the columns, which like the polarisation of muscles, nerves and the organ of Malapterurus, is under different circumstances sometimes relatively positive, sometimes relatively negative, the conditions required for the appearance of both polarisations being generally the same in the latter as in the former. With a long closing time, polarisation is in all circumstances relatively negative ; with a short closing time, particularly of stronger currents, relatively positive polarisation arises under certain conditions. Under certain other conditions which cannot be intentionally brought about, action in two directions results—first negative then positive, thus proving that here also negative polarisation is the more transitory. As the functional activity diminishes positive polarisation disappears, though it is a considerable time before it is quite absent and negative polarisation alone remains. All these effects are in general observed in equal strength to whatever part of the columns the clay points are applied, provided that they are kept at a constant distance. With a sufficient resistance of the galvanometer-circuit, which is secured by the leading-off clay points, these effects are the greater the greater the distance—in other words, we have to do with electromotive forces arranged in pile. Finally, with an oblique direction of the polarising-current along with an oblique position of the leading-off clay points, only weak results in indefinite direction are met with. The proofs of this are put together in the Appendix.

The relations of polarisation to the direction of the polarising-current are so marked in all these experiments, that one cannot go into detail as to the phenomenon without first entering on this point. My experiments had generally the same form as those on the upper and lower half of the group of muscles, or on the anterior and posterior roots of the spinal nerves[1], that is to say the homodromous and heterodromous currents are sent alternately through the columns at definite intervals of time. The stronger the current and the longer the closing time, the greater the interval must be in order to give time to the preparation to return to a sufficiently natural condition for comparative observations[2].

[1] Sitzungsberichte, 1883, vol. i. pp. 363–383.

[2] Long continued series of experiments which have to be broken at definite intervals are the more fatiguing from the necessity of constantly looking at the clock to see whether the time for a fresh observation has arrived. After having

The tables in the Appendix do not require any further explanation than has already been given in the Memoir 'On secondary electromotive phenomena.' The numbers in the horizontal series indicated by *S*, are the deflections through the secondary current, those indicated by *P*, are the primary deflections. A glance at these series, e.g. at series 10, will show that in this and the following as far as 13, the homodromous current (↑) induces both absolutely and relatively positive polarisation, the heterodromous current (↓) absolutely positive and relatively negative. From here onwards polarisation by both currents becomes relatively negative, the heterodromous remains absolutely positive, the homodromous becomes even absolutely negative, but is at first much weaker than the absolutely positive but relatively negative polarisation due to the heterodromous current. As the preparation becomes exhausted this difference disappears more and more.

All the series of experiments with short currents sent in alternate directions take as a rule this course. Whether the observation begins with the homodromous or the heterodromous current, polarisation by both currents becomes sooner or later relatively negative—the sooner (that is after the smaller number of alternations) the longer the closing time, but if the closing time has a certain duration even the first homodromous current produces polarisation which is both absolutely and relatively negative. The same thing occurs when the functional activity of the preparation is too small. Here from the very beginning only relatively negative polarisation is obtained by both currents, but the homodromous polarisation is appreciably the weaker of the two. Thus the condition arises at once which with a better state of the preparation only gradually appears in the course of a long series of observations, viz. that 'the negative polarisation-current is always stronger in the direction of the shock.'

We have thus insensibly arrived at an important result. For these are the words in which Sachs summed up his researches on homodromous and heterodromous polarisation in the Gymnotus[1], and of which I had hitherto supposed and repeatedly said that they

occupied myself for several years with such experiments, I had at length an experimental Alarum clock made for me by Baltzar and Schmidt of Leipsic, which could be set to various periods so as to indicate to the observer by the stroke of a bell at intervals of 1, $1\frac{1}{2}$, $1\frac{2}{3}$, 2, $2\frac{1}{2}$, $3\frac{1}{2}$, 5 or 10 minutes, that the moment for a fresh observation was come, he having been warned by another signal.

[1] Untersuchungen, pp. 217, 218.

contradicted my results with Malapterurus[1]. Now that I constantly observed the same thing in the Torpedo that Sachs did in the Gymnotus, and at the same time saw how the phenomenon came into existence, scales fell from my eyes. Not only is there no contradiction between our results and those formulated by Sachs in the above words, but both can be deduced from one very simple assumption ; and as my results with Malapterurus are also in accordance with the same assumption, it may be asserted that in all three electrical fish the secondary electromotive phenomena are essentially the same, and in a certain sense are understood.

We are further led to this assumption by the observation that in all my experiments on Malapterurus and Torpedo the heterodromous current never induced relatively positive polarisation. Even polarisation in two directions, first relatively negative and then positive, is only seen in the homodromous currents. Let it be supposed that both currents polarise relatively negatively in equal degree, but that the strength of the homodromous current is so much greater than that of the heterodromous that the relatively positive heterodromous polarisation is constantly masked by the relatively negative, and all becomes clear as may be seen in Fig. 17.

The assumptions under which this figure is drawn are similar to those which illustrate Sachs' results in Table II of the book on Gymnotus. The diagram represents shortly what happens in a series of experiments in which, as in the series given in the Appendix, the two currents are sent alternately through a portion of the organ. The abscissal axis of course marks the time. The ordinates in each section correspond to the moment of closure of the galvanometer after the opening of the battery circuit. Above the abscissal axis they express positive polarisation and below it negative. The ascending arrow means that, the current being homodromous, the course of the curve of polarisation above the abscissal axis is absolutely and relatively positive, and below the abscissa absolutely and relatively negative. The descending arrow implies that, the current being heterodromous, the course of the curve of polarisation if above the line is absolutely positive, relatively negative, and if below it, absolutely negative, relatively positive. The resulting polarisation current which acts upon the galvanometer is represented in each section by the shaded space which lies between the curve resulting from the algebraic summation of both polarisations and the axis.

[1] Sitzungsberichte, vol. i. p. 395.

In accordance with the reality it is seen that at first both currents give absolutely positive polarisation (section 1 of the figure), the homodromous being the stronger. Then comes a period (section 2) in which, although both polarisations are still absolutely positive, the heterodromous is the stronger. In section 3 the homodromous polarisation is seen to be absolutely negative and distinctly smaller than the heterodromous. In section 4 the two polarisations approach equality.

I need scarcely point out that it was the phenomenon of section 3 which Sachs had seen, without having been aware of the two preceding, and which he described in words which from their apparent contradiction to my results caused me so much difficulty, viz. that 'relatively negative polarisation is always stronger in the direction of the shock.' There still remains however some

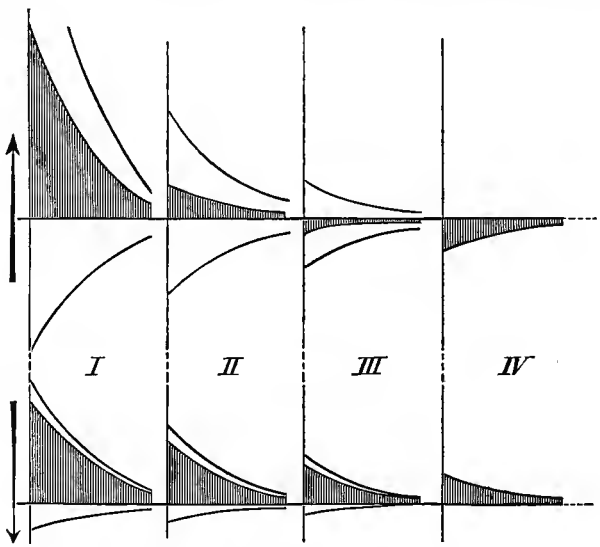


Fig. 17.

obscurity. Besides the polarisation experiments thus explained, Sachs has given others which are shown graphically in Plate II of the book on Gymnotus. In these experiments also polarisation by either current was without exception first relatively negative, but so strongly that the mirror shot out to the equator, in returning from which, according to Sachs' description, it swung several times on either side of the zero point. If the closing time exceeded a certain duration it swung twice over the zero point into the

relatively positive quadrant. The first of these two swings may be explained by the laws of the aperiodic movement of damped magnets. As the magnet fell from a height which exceeded the aperiodic district it was possible for it to pass the zero point, but only once[1]. The second movement in the same direction which Sachs also regarded as a swing, could only have depended on the change of sign of the resulting polarisation, provided that the mirror was really aperiodic. In the Gymnotus book I succeeded in drawing curves of the two polarisations, by combining which the resulting curves observed by Sachs could be deduced without much difficulty; but this was done under the assumption that both the heterodromous and homodromous currents induce relatively positive polarisation. This assumption is inconsistent with the conception which has now served to account for a much more numerous and better series of observations, including those of Sachs' own differently arranged experiments. The only traces of heterodromous relatively positive polarisation in the three electrical organs would be that second overpassing of the abscissal axis in some of Sachs' experiments. Under these circumstances I am led to believe that the latter were in fact what Sachs himself considered them to be, namely, oscillations. His galvanometer did not stand quite steadily[2], and perhaps his magnet was not well centred. In such a case a very strong current might throw the magnet into pendular oscillation to such an extent that it might overpass the zero point twice.

However this may be, the assumption which lay at the basis of my construction in the Gymnotus book, of the curves which express Sachs' empirical results, cannot now be maintained, and it may be considered proved that in all three electrical organs the homodromous current induces relatively positive polarisation, if not exclusively at any rate far more strongly. Before we attempt to draw a conclusion it is desirable to take knowledge of other facts.

11. On the relative Strengths of the Homodromous and of the Heterodromous Current in the Electrical Organ.

In my experiments on polarisation in the organ of Malapterurus I had already been much struck with the different strengths of the homodromous and heterodromous currents. 'In fresh strips in which positive polarisation appeared in full force in the direction of the shock, the descending current (homodromous in the Malapte-

[1] Gesammelte Abhandlungen, vol. i. pp. 284, 324, 355.

[2] Aus den Llanos. Schilderung einer naturwissenschaftlichen Reise nach Venezuela. Leipzig, 1879, p. 198. Untersuchungen, p. 137.

rurus) was always considerably stronger than the ascending (heterodromous) in the relation of 100 to 112, 116, or even 125. In heated or dying strips the difference disappeared. This result could not apparently be attributed to anything but the existence during the continuance of the primary current of a positive polarisation of great electromotive force, comparable to that of several Groves' elements, which in the homodromous current added itself to the force of the battery. Strips of the organ vertical to the direction of the shock (therefore cut obliquely from the fish) yielded, under the influence for a short time of a battery of 30 cells, a weaker positive polarisation, which however was equally strong in both directions; and the strength of the polarising current gave a deflection in both directions to the same number of the scale[1].'

So far had I arrived in 1857. How full of significance did it now appear to me when in almost every experiment on the Torpedo the superiority of the homodromous current manifested itself even in a higher degree than in Malapterurus. Series 13 and 14 are striking instances in point, for here the homodromous current of 30 Groves often appears more than twice as strong as the heterodromous. To explain this by a positive polarisation belonging only to the homodromous current, while an equal strength is attributed to the negative polarisation following each current, we should have to ascribe to the homodromous positive polarisation an electromotive force of more than 15 Groves. In series 20, with 50 Groves in the circuit, the relation between the heterodromous and homodromous current is at first nearly 3 to 5; the positive polarisation must have attained a strength of 20 Groves. In series 10, with 20 Groves, the same relation is as one to three; the secondary electromotive force in this instance is indeed only equal to about 13 Groves, but it must have amounted to double the primary.

When the current is directed transversely in the preparation there is no difference between the two currents, and the same remark holds good when the preparation is exhausted or has been killed by boiling temperature (see Sect. 12, and series 17 and 18 in the Appendix). In exposed preparations the difference can be observed to diminish as the preparation gradually dies.

We unfortunately as yet know nothing certain about the electromotive force of electrical fishes, except that it must be very considerable, least so, however, in the Torpedo[2]. At all events it is

[1] Gesammelte Abhandlungen, vol. ii. p. 720. Untersuchungen, pp. 206, 218.

[2] Untersuchungen, p. 276. Anm. 2. 411.

at the first glance incredible that so large an electromotive force should prevail in our preparations of organs, and another cause must be sought for the different strength of the two currents.

A difference of current strength must depend upon one of two causes—either upon unequal electromotive strength or upon unequal resistance. It is conceivable that in the electrical organ an irreciprocal resistance may exist[1], i.e. that it may conduct better in the direction of the shock than in the other. Electrolytes conduct only in so far as they are decomposed; according to a well-established law, however, electrolysis is preceded by a similar arrangement of electropositive and negative elements, which arrangement we have taken as the basis of our explanation of the shock and of positive polarisation. If this arrangement occurred more easily in the absolutely positive direction or in this direction exclusively, it would be comprehensible why the organ should conduct the homodromous better than the heterodromous current. The dependence of the hypothetical irreciprocal resistance on the vital condition might be explained on the ground that the inequality of the resistance in the two directions was an expression of electrical properties of the organ molecules which depended on their life. Thus we see ourselves in face of a problem which often recurs in galvanism and generally remains unsolved, namely to discriminate whether an observed difference of current strength arises from a difference of electromotive force or of resistance.

In the present case one method of answering this question would consist in introducing into the primary circuit so considerable a resistance in addition to that of the preparation of the organ, that the latter should disappear. If then the difference between the two currents disappeared while that of the two polarisations remained, this difference would be proved to be due to difference of resistance. I planned an experiment of this kind, in which, besides the preparation, I introduced as resistance a tube bent twice at right angles, 71 centims. long and two millims. internal diameter, containing physiological (normal) salt solution. The ends of the tube were closed with clay and dipped into two vessels of zinc solution. The difference of current strength in the two directions disappeared, but unfortunately owing to the diminished functional activity of the preparation, that of the polarisation current was also absent. In this case nothing more could be done as to the

[1] Comp. Arthur Christiani, Beiträge zur Elektricitätslehre. Ueber irreciproke Leitung elektrischer Ströme, Berlin, 1876.

determination of this question, and I have not yet been able to repeat the experiment.

I took an opportunity of approaching the desired end in another way. Instead of observing the polarisation after opening the primary current, I tried to form some notion of it during its persistence, by short circuiting the preparation through the leading-off clay points and the galvanometer circuit. The battery consisted of 20 Groves; the galvanometer coil (S) of 5000 turns had to be placed at a great distance from the mirror in order to keep the deflections within due limits. The closing time amounted at first to 0″·0764, afterwards to 1″·024. The result was astonishing; for while the homodromous current through the galvanometer (P) appeared almost twice as strong as the heterodromous, the branch of the homodromous current led off through the galvanometer (S) appeared very much weaker than that from the heterodromous (Series 25). When I replaced the preparation by a model of physiological clay (a much worse conductor, by the way) the difference had disappeared—a proof that irreciprocal resistance did not exist anywhere in the circuit.

It thus seems settled that the difference depends upon irreciprocal resistance. For as it is not conceivable that with an equal resistance in the preparation the led-off branch of the stronger current should turn out to be weaker, one is led to suppose that this depends exclusively on the better conductivity of the preparation for the homodromous current. More precise considerations however, aided by a schematic calculation, teach that this view is not sufficient, and that at all events under the assumption taken as the basis of the calculation, the result must be different.

For the sake of simplicity we assume that both currents produce relatively negative polarisation of equal strength, but that relatively positive polarisation is produced only by the homodromous. We assume the electromotive force of both polarisations to be proportional to the density of the battery current in the preparation, taking the transverse section and the length as each severally = 1. We will first enquire into what happens when the specific resistance of the preparation is unequal, as we thus avoid the complication which would arise from the assumption that the difference of resistance in the two directions may be a function of the current density. This assumption, though well worthy of consideration, is very difficult to express mathematically. Also we look upon the preparation as a linear conductor, or as if both the dorsal and

ventral surfaces rested upon metallic non-polarisable electrodes, with which the ends both of the battery circuit and of the galvanometer circuit were in connection. See Fig. 18, *A* and *B*, which represents the state of things for the homodromous and heterodromous currents respectively. The battery circuit with the battery are indicated by Σ, the galvanometer by (*P*), the galvanometer through which the branch is led off by (*S*). The branches of current which proceed from the battery are indicated by unbroken arrows, those of the absolutely positive polarisation by broken arrows, and those of the relatively negative polarisation by dotted arrows. It is unnecessary to remark that in this rough sketch we take no account either of the duration of polarisation, or of induction.

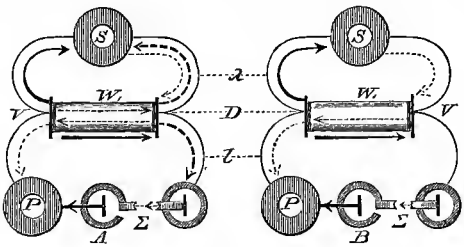


Fig. 18.

Let *E* be the electromotive force of the battery: *l*, the resistance of the battery circuit containing the battery and the galvanometer (*P*); λ, the resistance of the galvanometer circuit containing the galvanometer (*S*); *w*, *w'*, the resistance of the preparation when the current is homodromous or heterodromous respectively; *K*, the sum of the products $wl + w\lambda + \lambda l$ with the homodromous current, according to Kirchoff; *K'*, the corresponding sum with the heterodromous current. Let *P* be the constant by which the current density prevailing in the preparation must be multiplied in order to give the electromotive force of the homodromous absolutely and relatively positive polarisation; Π, the corresponding constant for the relatively negative polarisation; *I*, the strength of the homodromous current in the battery circuit; *I'*, that of the heterodromous; *i*, and *i'*, the corresponding strengths of current in the circuit derived through the galvanometer.

In the battery circuit there prevails a current strength of $E(w+\lambda)/K$ which is due to the electromotive force of the battery. To this is added whatever amount of current exists in the battery circuit in consequence of the polarisations. The battery circuit has

in the preparation the strength of $E\lambda/K$. Therefore the polarisation induced (as the transverse section $= l$) is $(P-\Pi)E\lambda/K$, and the branch current which originates in consequence in the column current $[(P-\Pi)E\lambda/K]\times[\lambda/K]$. As in this circuit P and E are in the same direction, we have

$$I = \frac{E}{K^2}[(w+\lambda)K+(P-\Pi)\lambda^2].$$

As in the galvanometer circuit P and E counteract one another, we have

$$i = \frac{E}{K^2}[wK-(P-\Pi)\lambda l].$$

I' and i' are obtained respectively from I and i, by making $P = 0$ and by transforming wK into $w'K'$. Accordingly

$$I' = \frac{E}{K'_2}[(w'+\lambda)K'-\Pi\lambda_2], \quad i' = \frac{E}{K_2}[w'K'+\Pi\lambda l].$$

By observation it is known that $i<i'$, $I>I'$, thus we have the inequality

$$I-i>I'-i', \text{ or}$$

$$K'_2[K+(P-\Pi)(\lambda+l)]>K_2[K'-\Pi(\lambda+l)] \ldots\ldots\ldots (*).$$

The first question now is whether, according to our surmise, this inequality is fulfilled by $w'>w$ when $P = 0$, which would imply irreciprocal resistance in the preparation without absolutely positive polarisation. Certainly this is the case. If you make $P = 0$, and for the sake of shortness $\lambda+l = a$, $\lambda+l = \beta$, the inequality may be written thus:

$$(w'-w)[(\beta-2a\Pi)(\beta+a(w'+w))+aw'w]>0.$$

For this condition is satisfied by $w'>w$, so long as the quantity within the square brackets does not become negative. This can only happen if the constant Π of negative polarisation exceeds a certain value, which is for the moment of no interest to us.

Now, on the other hand, it may be asked whether, according to the other part of our surmise and the conclusion we arrived at *prima facie*, the inequality may not also be fulfilled when $w = w'$, when P is not $= 0$ as above, but of finite positive magnitude. Inasmuch as it is obvious that the inequality (*) holds good so long as $P>0$, that is to say, provided that homodromous absolutely relative polarisation exists, the phenomena may present themselves just as we observed them even without irreciprocal resistance. Thus we have arrived at no conclusion; the predominance of the homodromous current can be explained as well by positive polarisation as by irreciprocal resistance.

Naturally the conception remains possible that both explanations have a foundation in fact; it certainly is so if irreciprocal resistance is in question; for there can be no doubt of the existence of positive polarisation, whereas irreciprocal resistance is a new property attributed to the organ, the existence of which along with positive polarisation still requires proof. Until this proof is given, it must be assumed that in an organ preparation of scarcely the size of the well-known group of muscles of the frog, there is always an electromotive force of 20 Groves. It will be easier to believe this when one remembers that in the organ of the living fish when giving a shock, a much greater electromotive force is undoubtedly in operation. But when the force of this organ is brought into conflict with a known force like that of Groves' battery, the astonishing value of this fact is impressed more forcibly upon us. It has indeed only one counterpart, the surprising nature of which we are apt to overlook, namely, the mechanical activity of which the few grammes of water and organic substance which here act electrically are capable when they take the form not of an electromotive organ, but of muscle[1].

What gives in addition special interest to the experiments just described, in which the preparation is short circuited during the continuance of the current by the galvanometer circuit, is the circumstance that Sachs made a similar experiment on Gymnotus with, so far as can be judged, the same result. He kept the current of his seventeen Groves closed through a bit of organ, and led off a branch with the clay points through the galvanometer, the sensibility of which was suitably diminished. 'When the current was led through the organ in the direction of the shock, the deflection amounted to 80 sc., in the other direction to 95 sc. The deflection remained constant at this point[2].' Thus Sachs only observed i and i', as the means for observing I and I' were wanting. As therefore he found, as I did in the torpedo, $i < i'$, it is very probable that he would also have found $I > I'$.

12. Dependence of the Secondary Electromotive Effects and of the Conductivity of the Organ on its Vitality.

It has already been pointed out several times that the polarisability of the organ is intimately bound up with its vitality. I have not yet made methodical experiments as to this dependence, and they would be difficult to carry out for the reasons given on p. 445. The

[1] Comp. Monatsberichte der Akademie, 1858, p. 99. [2] Untersuchungen, p. 218.

dead organ only shows weak relatively negative polarisation which is equally strong in the two directions. The same fact is observed in a preparation which has been boiled. The organ was no longer fresh; it had lain on ice for forty-eight hours, the air being of a moderate summer temperature. The organ showed an alkaline or neutral reaction to litmus paper, but after a sudden scalding and boiling it became acid and turned the paper decidedly red. In this respect therefore it manifested the same difference from muscle as the organ of Malapterurus[1]. The columns of the boiled organ separated from one another at the slightest touch. In this condition the preparation had lost every trace of organ current. Before the boiling, the current of 30 Groves being closed for 5″, the relatively negative polarisation was so strong that the scale disappeared from the field; after the boiling only a trace in the two directions resulted. Thus it looked very much as if the resistance of the preparation had diminished, just as I found to be the case in muscle and in the tissue of plants[2], and as I had also stated with regard to the organ of Malapterurus[3]. The current strengths before and after boiling were in the proportion of about 100 to 133; but as in boiling some of the columns had been separated the proportion was undoubtedly smaller. Whether the dead organ, like dead muscle, conducts better than the fresh, I could not determine, but it is very probable, on account of the acid reaction which appears as the organ dies.

13. Discussion of the foregoing Results.

However incomplete the experiments above given as to the secondary electromotive phenomena of the electrical organ may

[1] Archiv für Anatomie, etc., 1859, p. 846. Gesammelte Abhandlungen, vol. ii. pp. 17 ff., 646, 647. Untersuchungen, pp. 70–72.

[2] Comp. J. Ranke, Tetanus. Eine physiologische Studie, 1865, p. 16. Gesammelte Abhandlungen, vol. ii. pp. 95, 118.

[3] Sitzungsberichte, 1883, vol. i. pp. 392, 398. By an error it is there stated that a strip of Malapterurus organ has its resistance diminished by boiling, from 100 to 42. It ought to be, as above in the text, that the strength of the current is raised by boiling in the proportion of 100 to 238. That the proportion of the current strengths before and after boiling was less in the case of the Malapterurus than in that of the Torpedo arose from the circumstance (in addition to that given in the text) that the conducting vessels with club-shaped pads and films of albumen, then used for leading off, had a smaller resistance than the conducting tubes with clay points which were employed later. But for this very reason, this proportion, in the experiments on Malapterurus, approached more nearly to the actual (reciprocal) proportion of the resistances of the preparation.

be, they serve as the foundation of a considerable advance in the knowledge of this organ. In place of the annoying discrepancy between Sachs' results with Gymnotus and mine with Malapterurus, we see that in all the three electrical fish the secondary electromotive phenomena of the organ are the same. It has been possible to follow these phenomena more in detail in the Torpedo than in Malapterurus, and still more completely in Gymnotus. The mere fact that the Torpedo organ, instead of being scarcely available for these experiments, turns out to be well adapted to them, is of great value, and in connection with the prospect of having at our disposal in this laboratory living Torpedos, gives reason to hope that what was only roughly sketched out in haste may be more completely investigated. It might perhaps be advisable to postpone till then the discussion of what has been already gained. It cannot do harm, however, to set forth the actual condition of things, and to indicate the chief points of view which have next to be taken. The relatively negative polarisation, equally strong in the two directions, which simply increases up to a certain limit with the density and duration of the current, we will for the present consider as ordinary internal polarisation, although as in muscle and nerve its dependence upon vitality and its destruction by a boiling temperature raises some doubt.

Our newer experience leads us to regard it as much more difficult to form an idea of the nature of the absolutely positive polarisation which is even provisionally satisfactory. There can be no doubt that, in opposition to relatively negative polarisation, it appears as if it were the more physiological process of the two. Its dependence on vitality is greater, it is the first to disappear when the organ dies. There are, however, two different ways of considering it. The first consists in looking upon it along with the organ current as the after-effect of a shock liberated by electrical excitation; the second in considering it as the consequence of a pile-like arrangement of the electromotive molecules determined immediately by the homodromous current.

At first sight there appear to be strong grounds for accepting the former explanation. As we explain the shock itself by a pile-like arrangement of electromotive molecules, it may be asked how this arrangement may be distinguished from that indirectly generated through the homodromous current (corresponding to absolutely positive polarisation) and why the latter should not always assume the character of a shock. The second interpretation, according to

which absolutely positive polarisation may be indirectly affected by the homodromous current but not by the heterodromous, attributes a new and obscure property to the organ. Indeed the first interpretation has something of a similar character in so far as it is assumed that only the homodromous current liberates the shock. But we can account for the same series of phenomena which Fig. 17 was intended to illustrate, if we admit that a shock may be generated by the heterodromous current along with relatively negative and absolutely positive polarisation. It must indeed remain much weaker than that through the homodromous current, but for this the law of contraction offers an analogy.

So much doubt, however, is attached to the first explanation that I cannot unreservedly agree to it. It is to be remarked besides that it rests upon a supposition which we made on account of its simplicity, but which is still unproved, namely, that the heterodromous current is incapable of generating relatively positive polarisation. All that is certain is that such polarisation has not yet been seen, but it may have been constantly masked by relatively negative polarisation, because weaker than the homodromous absolutely and relatively positive. This is indeed the conception which lies at the base of our construction in Fig. 17.

Thus it is by no means so certain that there may not be two conditions, both connected with the pile-like arrangement of the molecules, which are the same in their external effect, but different as regards what happens in the interior of the electrical plate, one corresponding to the shock, the other to absolutely positive homodromous polarisation. The organ-current no less than the after-effect of the shock, according to the first assumption, demonstrates that every absolutely positive effect is not a shock.

It sometimes comes about, however, in series of experiments with fresh preparations that at first an action follows so exceptionally strong that the scale shoots out of sight, and in this the after-effect of a shock, if not the last portion of one, may undoubtedly be recognised. This phenomenon presents quite a different aspect from the ordinary absolutely positive polarisation which is experienced when observations are frequently repeated on the same preparation, inasmuch as it does not show a persistence proportional to its original strength. A similar succession of phenomena are observed in the after-effects of shocks liberated by mediate excitation of the preparation such as cutting off protruding ends of nerve trunks. The way in which the absolutely positive deflections gradually and

slowly decline in strength with a regularity which perfectly corresponds to the nature of the shock and the functional activity of the preparation, and finally fade away, affords no countenance to the impression that we have here to do with a process of discharge allied to muscle twitch.

This is the place to mention a point not yet expressly dealt with, and which, although of great importance, has not been by any means sufficiently explained in strict relation to facts, namely, the dependence of absolutely positive polarisation on current density. Although I had long believed that the threshold of current density for the generation of this polarisation must be high, I only discovered too late with the preparations from the last fish sacrificed, that under certain circumstances even the currents from one Grove generated absolutely positive polarisation, with the peculiarity, however, that this effect speedily came to an end, a fact which had probably deceived me before. If now the number of elements was suitably increased, the ordinary effects reappeared (Series 1). The variable phenomena which pressed upon me were so numerous that I was unable to come to a certain conclusion. A very curious movement of the mirror recurred from time to time without my being able to penetrate into its meaning, still less to produce it at will, namely, that the image of the scale instead of retreating from the maximum deflection as usual was thrown back with a jerk.

A method of experiment suggested itself to me too late, by the aid of which, when I have again Torpedos at my disposal, a successful discrimination between the two conceptions of absolutely positive polarisation which have been contrasted with each other, ought to be possible. The experiment consists in tetanising the organ preparation by alternate currents instead of subjecting it to a single current impulse. I began at once to set this going by closing the secondary circuit[1] of the inductorium with the 'Wippe' instead of the battery circuit. If the absolutely positive polarisation is nothing more than the after-effect of the shock, it ought to appear with the greatest possible strength after tetanising for a short time. This was, however, not the case. Even when the induction was extremely strong, with the ordinary arrangement of the inductorium only weak polarisation followed, the direction of which was such as would have resulted from exclusively opening shocks; that is to say, the polarisation was absolutely and relatively positive when the opening shocks were homodromous,

[1] See p. 489, note.

and relatively negative but absolutely positive when they were heterodromous. After long-continued tetanus of the gymnotus organ Sachs found that the tetanus current was weakened rather than strengthened, as is the case after a single shock (see above, p. 445). But this does not explain the result of my experiment. Unfortunately up to the present I have only been able to make it a few times, with an organ in impaired state of functional activity, so that I cannot altogether trust its result.

There is still one method of experiment at hand which under certain conditions might lead to the attainment of the object, that is to observe whether with a longer closing time the homodromous current maintains its ascendancy. If this is the case, positive polarisation cannot be identified with the shock, for the latter, when a constant current goes for a long time through the organ, can only add itself to the battery current at the moment of closing. I have in fact seen this ascendancy with a closing time of 1″, 5″, or even 20″ (Series 8, 15, 16, 25); but experiments of this kind will not be conclusive until the hypothesis of an irreciprocal resistance is completely set aside.

It is obvious that nothing remains but to set oneself patiently to further investigations, the road to which is, however, clearly indicated. The next consignment of Torpedos will bring us a step nearer to the determination of the present question.

14. On the electromotive Actions of the Electrical Nerves of the Torpedo.

The only researches as to the electromotive actions of electrical nerves which had hitherto appeared were those which I had made on the Malapterurus. The nerve showed no current between the longitudinal and transverse section when at rest, and no negative variation in tetanus; but with two Groves it gave weak but undoubted indications of electrotonus currents[1]. Its functional activity was already considerably diminished; it would not, however, be surprising if even the perfectly fresh nerve gave neither rest current nor negative deflection, for the transverse section of the single fibre which runs in the axis of the nerve, bears to the total transverse section a relation varying from 1 : 90 to 1 : 104[2]. In consequence of this extraordinary peculiarity in the construction of the electrical nerve of Malapterurus, the result is just as if no

[1] Gesammelte Abhandlungen, ii. p. 645.

[2] Ibid., ii. p. 645. N.B. A misprint here puts 8950 for 89.50.

electromotive observation had been made with respect to electrical nerves; and unfortunately Sachs let the opportunity pass by of filling up the gap by his observations on Gymnotus[1].

Even the Italian electrophysiologists did not make use of the advantages offered them by Nature, and so it was, strange to say, reserved for me more than forty years after the discovery of the nerve-current, in the Physiological Institute of this northern metropolis, to bring Torpedo nerve for the first time into the galvanometer circuit. This occurred on the first occasion that I had the opportunity of killing a Torpedo, viz. on the 13th of June of last year. As it was uncertain how long the nerves would remain alive in summer temperature, I begged Prof. Christiani to undertake this investigation while I occupied myself with experiments on polarisation in the organ. Professor Fritsch was so kind as to prepare for experiment the nerves with which he was so familiar.

The eight electrical nerves of a large torpedo, four on each side, form, as I had anticipated, an excellent object of investigation[2]. They are easily prepared without branches, as long as from three to 4 cm., and at an average thickness of 2·5 mm. Even if they do not as electrical nerves differ from other nerves, they will afford the means of obtaining solutions hitherto unattainable of problems in the general physics of nerves.

1. *Current of rest of the Electrical Nerves of the Torpedo.*

Shortly before undertaking the measurement of electromotive force in the electrical nerves, a similar measurement with the same apparatus was made of the N. ischiadicus of the frog, and yielded the ordinary values of 0·014 to 0·022 Rauolt. The portions of electrical nerves were of the same length as those of the ischiadicus, viz. 12 to 15 mm. From the greater thickness of the former it might be expected that with an equal specific electromotive force there would be a greater galvanometric effect. This was not the case. Christiani obtained the following numbers from the electrical nerves:—

I.	II.	III.	II b.
0·0054	0·0086	0·0054	0·0089

The number under II b relates to another animal used on the 27th of June. The greatest force obtained by Prof. Christiani is more than twice as small as that of the nerves of the frog, more than

[1] Untersuchungen, p. 171. [2] Wiener Sitzungsberichte, 1883, i. p. 387.

three times as small as that of the nerves of birds, or of mammalia with the exception of those of the horse, and over five times as small as that of the nerves of the lobster, as determined by Fredericq[1].

This striking result demanded further experimental proof, which in the course of the winter I carried out on two Torpedos. In consequence, perhaps, of the cold and hunger from which the creatures had suffered for more than two months, the average value which I obtained was still less than that of Christiani. The mean of his four measurements is 0·007075, of my sixteen only 0·005925. In only one case I obtained a higher value, namely, in a very fresh fish, in which the force reached 0·01123, an amount observed even in weaker nerves of the frog and of the toad, notwithstanding that they are much thinner[2]. In so far as my measurements simply confirm those of Prof. Christiani, I would not dwell further upon them, had I not come in the course of them upon a point relating to their behaviour, which seems sufficiently important to represent in the following table :—

ELECTROMOTIVE FORCE OF THE ELECTRICAL NERVES OF THE TORPEDO IN RAOULT.

			Between Equator and		*Between the Two Transverse Sections (P–C).*		
			Peripheral Transverse Section (+P, ↑).	*Central Transverse Section (+C, ↓).*	*Observed (D).*	*Calculated (Δ).*	*D – Δ.*
Third Torpedo, 29 cm. long, killed 13/xii/83.	L	IV.	0·00529	0·00284	—	—	—
		III.	0·00658	0·00400	—	—	—
		II.	0·00724	0·00458	+0·00160	+0·00265	−0·00105
		I.	0·00366	0·00185	+0·00194	+0·00181	+0·00013
	R	I.	0·00699	0·00489	+0·00119	+0·00210	−0·00091
		II.	0·00680	0·00583	+0·00105	+0·00097	+0·00008
Fourth Torpedo, 25 cm. long, killed 28/xii/83.		I.	0·01123	0·00970	+0·00150	+0·00153	−0·00003
		II.	0·00757	0·00577	+0·00187	+0·00180	+0·00007
		Trigeminus branch.	0·00361	0·00301	+0·00195	+0·00060	+0·00135

[1] Archiv für Physiologie, 1880, pp. 68, 71.

[2] Comp. Wedenskii, Notiz zur Nervenphysiologie der Kröte. Archiv für Physiol. 1883, p. 310.

The Roman figures are the numbers in order of the electrical nerves, L and R stand for left and right, the rest of the table speaks for itself. It is seen that in these experiments the peripheral transverse section shows greater negativity as compared to the equator. Having been struck by this in the two first experiments, I thereupon led off the bit of nerve with the clay shields from the two transverse sections. The last column shows how exactly the force so obtained corresponds with the difference of forces between the equator and the two transverse sections.

In order to test the correctness of the rule thus discovered, I begged Prof. Fritsch to mark one end of the bit of nerve with a thread of coloured silk, and to hand me the portion without telling me which end was central and which peripheral. Without exception I indicated this correctly on the first glance, guided by the ascending direction of the current in the nerve from section to section. Even between symmetrical points of the longitudinal surface in the neighbourhood of transverse sections the ascending current could be observed. It would be important to investigate it in uninjured nerves.

The first occasion on which this fact was seen was when the Torpedo had been killed, as described on p. 438, by punching out the electrical lobes; and as I did not arrive at the investigation of the nerves till some time later, there was a possibility that the smaller negativity of the central transverse section as compared with the peripheral might be due to the progressive exhaustion of the nerve. In the fourth Torpedo, which yielded the figures given in the three last rows of the Table, I obviated this suspicion by not removing the brain. I made instead a sagittal incision with the knife mentioned on p. 440 at some distance from the gills, and immediately after, a second cut through the gills themselves close to the skull. Between these two almost simultaneous incisions lay the portion of nerve, both transverse sections of which were equally fresh. In this case there could be no question of the difference being due to exhaustion, and yet the electromotive difference was as marked as it was regular. Even in a nerve branch detached from the organ, and so distant from the centre that the local exhaustion could not as yet have reached it, I found the ascending current between the two sections.

Some years ago (1867) I came on traces of a similar law in the sciatic nerve of the frog, but I arrived at no conclusion; the greater number of my experiments indicated that here the central

transverse section was the more negative, the nerve being permeated from section to section by a descending current. It is obvious that this investigation must be resumed as regards various nerves, both centripetal, centrifugal, and mixed. It will then soon be manifest with what we have to do—whether with a peculiarity of electrical nerves, whether with a fundamental law connected with their centrifugal function, or finally, with a less essential difference common to all nerves, dependent only on relations of nutrition. The result seen in the sciatic of the frog, a nerve of mixed function, seems to show that function is not without influence. The last records in the table, of the trigeminus branch, are only in apparent contradiction with this idea, in so far as this branch being a secretory nerve may be also regarded as centrifugally active. On the other hand this experiment seems to show that the greater negativity of the lower transverse section is not peculiar as such to electrical nerves, as indeed was improbable.

It remains to be asked what connection there is between this and the small electromotive force of the electrical nerves of the Torpedo. The experiment on the trigeminus branch seems to show that this peculiarity in them is not due to their electrical function. Yet it is possible that it is connected with the electrical immunity of the Torpedo and with the high excitatory limen of its muscular nerves, as proved by Boll[1]. Further investigations on this point are necessary. A few experiments made at the same time on the optic nerves of the carp and pike yielded no result worth recording.

2. *Negative variation of the current of the Electrical Nerves of the Torpedo when in a state of activity.*

The nerve marked II in Christiani's experiments above mentioned was in contact with the electrodes by a longitudinal and cross section, and kept the thread at 60 of the scale. By means of the round compensator the thread was brought back to zero. When the nerve was tetanised by means of the inductorium, Christiani obtained a negative variation to the amount of 5 sc., that is, $\frac{1}{12}$ of the original current strength. In another case, in which the nerve had already been used for electrotonus experiments, the compensated deflection amounted to 120 and the variation to 90 sc., fully $\frac{3}{4}$ of the current strength. When the nerve was divided between the

[1] Untersuchungen, p. 265.

two pairs of electrodes and joined together again, no effect was produced by tetanising it.

I made a similar experiment on the nerve marked R I. in the Table, and obtained with a deflection of 52 sc. (Helmholtz' arrangement) negative results as follows :—

With a distance of coil of 100 mm. the deflection was 0,
" " 50 " " 2,
" " 25 " " 5 sc.;

that is to say, a variation of $\frac{1}{10}$. When a woollen thread steeped in sea-water was substituted for the nerve no effect was seen. So far everything was regular, but it is strange that both Christiani and I observed, in addition to the regular negative variation, a quick, positive, initial jerk, and I twice saw a similar terminal jerk, so to speak. These positive jerks of the mirror could not be attributed to errors in the arrangement (such as escape of current, action at a distance or the like), because they were observed first by Christiani and then by me, after half a year's interval of time and with altogether different apparatus, and because no effect occurred when the nerve was divided, or when a moist woollen thread was substituted for it. Whether this indicates some peculiarity of electrical nerves must be decided by further investigations. However this may be, with regard to this unexpected collateral effect and with regard to the search for the supposed fundamental errors of experiment, an observation was neglected (a failure which will now be repaired), viz. that of the propagation of the variation in two opposite directions in a nerve acting purely centrifugally. Corresponding observations were afterwards made by me on the spinal nerve roots of the frog[1].

3. *Electrotonus currents in the Electrical Nerves of the Torpedo.*

In the investigation of electrotonus currents in electrical nerves, Christiani also met with irregularities, which for the present can be ranged under no certain law, and which require further researches for their explanation. In the fourth right nerve of the fish killed on the 13th of December, the total length of the three tracts being 10 mm., I observed with from one to five Groves in the electrotonising current, that the anelectrotonic and kathelectrotonic augmentations appeared regularly, the first rising up to a certain point and then gradually diminishing, the latter sinking immediately. When the nerve was divided and brought together again between the

[1] Untersuchungen über thierische Elektricität, ii. pt. i. p. 589.

excited and led-off tracts, weak and sometimes reversed effects remained, attributable to current escapes which, owing to the thickness of the nerve, could not altogether be avoided. The absolute amount of the augmentations observed was so considerable that 10,000 turns and a distance of 50 mm. from the mirror gave suitable deflections: their relative amount could not be determined for want of a point of comparison. Observations of the spread of electrotonus in directions alternately centripetal and centrifugal were unfortunately neglected. Such observations were made in Christiani's more numerous experiments, but the irregularities above mentioned appeared in both directions, and once more nothing remains but to await patiently the results of new experiments.

The experiments as to the polarisation of the electrical nerves have not been carried far enough to allow of anything certain being communicated. I have not yet found time to measure the electromotive force of the muscles. It is to be hoped that a fresh consignment of Torpedos in the spring will afford opportunity to carry out more thoroughly and conveniently the investigations here mapped out than was possible in the first instance, as well as to undertake experiments of time measurement.

APPENDIX.

In the following Tables, which contain only a part of the results of my experiments, the Roman figures indicate the number of Groves, *C T* stands for the closing time, *O C* for the force of the organ current, *L* for the length of the columns of the preparation of the organ, *P* (period) the time between each two immediately following experiments. The mark ‖ means that the experiment was continued on the same preparation under the new conditions given. The deflections (with the exception of those in series 25 where this would have had no meaning) are reduced to the deflection which would have been caused by an equal current strength in galvanometer (*S*) with a bobbin of 5000 turns at a distance of 30 mm. from the magnet; all the deflections in galvanometer (*P*) are reduced to the deflection which would have been produced with 50 turns at a distance of 20 mm. This explains the large numbers which appear when the currents are of great strength and persistence, and which go far beyond the limits of the scale[1]. $500+x$ stands as before for a deflection beyond the limits of the scale, which consequently could not be reduced; a stroke in place of an entry shows that from some cause or another the observation failed; *O C*, *L*, and *P* are sometimes not indicated.

The figures 1 .., 2 .., &c. Torp. correspond to the order of the days on which the animals were killed—June 13 and 27, Dec. 13 and 28 of last year, and Feb. 2 of this year. In the same order the lengths of the fishes were respectively 29, 36, 29, 25, 26 cm. The word 'fresh' indicates that the experiment was made on the same day on which the animal was killed; '2 ., day,' on the day after.

1.

5. Torp. 2. Day. *OC* still positive.

CT 0″.0764.

I.–*S.*	↓	−234	↑	+80; +10	↓	−4	↑	+3	↓	0	↑	0; 0;	‖	X.	↑	+22	↓	−15	↑	+25	↓	−50	↑	−12	↓	−34
P.	↓	4	↑	9·75	↓	4·5	↑	5	↓	4·5	↑	8; 8·5	‖		↑	82	↓	71	↑	78	↓	75	↑	79	↓	69

This series shows that the homodromous current with only one Grove may generate absolutely and relatively positive polarisation, but only for a short time, after which a stronger current acts in the usual manner.

[1] Gesammelte Abhandlungen, p. 356.

2.

As in Series 1.

CT 0″.0764.

II.—*S.*	↑	+357	|	−110	↑	+85	|	−5	↑	+74	|	−0·5	↑	+62	| 0	||	| −85
P.	|	7·5	↓	7	|	8·5	↓	8·5	|	8	↓	7·5	|	7·5	↓ 8	||	↓ —

This series appears to show that, with short closing time of a weak current, relatively negative polarisation disappears so soon that almost nothing is left but homodromous absolutely and relatively positive polarisation.

3.

3. Torp. 2. Day. *OC* 0·0129. 2-′*P.*

CT 0″.0063.

V.—*S.*	↑	+500	|	−350	↑	+190	|	−118	↑	+160	| −179
P.	|	+*x* 5·5	↓	2·25	|	4·2	↓	3·6	|	4·2	↓ 2·8

This series shows that under certain circumstances, with even five Groves, positive and negative polarisation are beautifully produced.

4.

2. Torp. Fresh. *L* 23 mm. *OC* 0·0145. 2-′*P.*

CT 0″.0764.

V.—*S.*	↑	+35	|	−126	↑	−	|	−122	↑	{ −3 +15 }	|	−70	↑ +28
P.	|	29·5	↓	23[1]	|	28	↓	24·5	|	28	↓	24·5	| 28

Here the less favourable result in spite of more favourable conditions can scarcely arise from the closing time having been more than ten times as long, but must have been caused by the unontrollable irregularities of the experiment. The effect in both directions of the third homodromous current impulse is to be noted.

5.

4. Torp. Fresh.

CT 10″.580.

V.—*S.*	↑	− 200	|	−190, &c.
P.	|	500 + *x*	↓	485 to 471

Only negative polarisation results from a longer closing time. The polarising current sinks to a small amount during this period, in spite of non-polarisable electrodes.

6.

3. Torp. 2. Day. $2\frac{1}{2}$-″*P.*

CT 0″.0032. *CT* 1″.024.

X.—*S.*	|	−32	↑	+19	|	−54	↑	+40	|	−4	↑	+39	|	−3	↑	+35	|	−2	|| |	−113	↑ −79	| −94, &c.
P.	↓	8·2	|	8·2	↓	6·6	|	8·2	↓	6·6	|	6·6	↓	6·6	|	11·5	↓	6·6	|| ↓	301	| 318	↓ 318

In this series, in which the closing time was the shortest possible, it is seen that, as in series 2, negative polarisation subsides, whereas it alone keeps the field when the closing time exceeds a certain limit. It is striking, and reminds one of a twitch experiment to observe the increase of the effects during the first four alternations of the current.

X.—S.	+30	−140	+55	−50	+45	−42	+44	−30
P.	68·9	42·7	68·9	58·8	62·4	57·3	62·4	59

With a closing time ten times longer than in the preceding series but still short, negative polarisation already shows itself more strongly.

8.

3. Torp. Fresh. *OC* 0·0133. 3 −′*P*.

CT 21″·78.

X.—S.	−424	−260	−398	−270
P.	564 to 515	589 to 564	548 to 484	573 to 548

This series shows pure positive polarisation with a longer closing time, together with an appreciable sinking of the polarising current.

9.

3. Torp. 2. Day. *OC* 0·0044. $1\frac{1}{3}$ −′*P*.

CT 0″.0032.

XX.—S.	+31	−55	+57	−5·5; 6	+58	−3·5	44	−3	+50	−3·5, &c.
P.	12	6	14	6·5; 6·5	12	6·5	12	6	8·5	6·5

The same result as with ten Groves and the same closing time.

10.

2. Torp. Fresh. *L* 29 mm. 2 −′*P*.

CT 0″·0764.

												10
XX.—S.	+280	−45	+50	−45	+44	−34	+34	−57	+30	−52
P.	274	91	266	92	237	104	237	108	232	112
												20
S.	+26	−42	+23	−37	−9	−37	−10	−34	−14	−33
P.	232	104	224	125	208	125	195	125	195	125
												30
S.	−16	−30	−18·5	−28	−20	−31	−21	−30	−23	−29
P.	191	129	191	141	191	141	183	145	170	141

This series, in which thirty alternations of current at intervals of two mm. each, lasted for an hour, expresses very fully the law graphically represented in Fig. 17. After the 15th alternation the phenomenon of polarisation showed itself in the manner described by Sachs in the Gymnotus (see Sect. 10).

11.

2. Torp. 2. Day. *OC* 0·0045. 2 −′*P*.

CT 0″·0764. *CT* 21″·78.

X.—S.	+520	−140	+65	−95	+31	−1509	−355	−1161	−606	−954	−632
P	—	72	154	77	147	929 to 864	1161 to 1071	1161 to 1079	1393 to 1213	1316 to 1218	1548 to 1342

The experiments with a short closing time were merely a repetition of the foregoing series, and serve to show that the preparation was still in a condition of activity. The deflections of the galvanometer (P) with the longer closing time correspond well with those obtained in series 8, in which only 10 Groves were used and the closing time was the same. The increase of the deflections as the experiment proceeded depended on the heating of the preparation. The deflections due to negative polarisation are remarkably large in the last half of this series.

12.

1. Torp. 2. Day. OC 0·0059. $2\frac{1}{2}-'P$.

CT 0″·0629.

XXX.—*S.*		−58 ↑	+99		−50 ↑	+50		−40 ↑	+28		−38 ↑	+12		−34
P.	↓ 239		260	↓ 256		267	↓ 260		260	↓ 260		256	↓ 253	

Essentially the same results are here repeated.

13.

2. Torp. Fresh. L 20 mm. OC 0·0090. $2-'P$.

CT 0″·0764.

XXX.—*S.*		−128 ↑	+80		−134 ↑	+130		−73 ↑	+49					
P.	↓ 134		284	↓ 146		262	↓ 151		268					

14.

2. Torp. 2. Day. L 17 mm. OC 0·0053. $2-'P$.

CT 0″·319.

XXX.—*S.*		−500−x ↑	+1·0		−325 ↑	+56		−115 ↑	−10		−150 ↑	−37		
P.	↓ 370		790	↓ 376		766	↓ 370		684	↓ 380		654		

15.

2. Torp. Fresh. L 14 mm.

			CT 1″·024.									CT 5″·202.			
XXX.—*S.*	↑	+150*		−500−x ↑	−145		−500−x ↑	−190	‖	↑	−500−x		−500−x		
P.		1712	↓	1012		1326	↓	1012		1064			—	↓	5475

The remarkable phenomenon which presented itself here, viz. the very slow development of the absolutely and relatively positive deflection (*), was obviously caused by the considerable diminution of negative polarisation, which however did not in this case occur with sufficient rapidity to give occasion for a deflection in successively opposite directions.

16.

1. Torp. Fresh. L 12 mm. $3\frac{1}{3}-'P$.

CT 5″·202.

XXX.—*S.*	↑	−2288		−3840 ↑	−2247		−2105
P.		2886	↓	3105		3461	↓ 2434

17.

1. Torp. 3. Day. L 15 mm. OC? 2–'P.

CT 0″·0629.

XXX.—S.	↑ −87	−84 ↑	−90	−89
P.	513 ↓	513	544 ↓	560

The exhausted organ no longer gives positive polarisation.

18.

1. Torp. Fresh, but scalded. $2\frac{1}{2}$–'P.

CT 5″·202.

XXX.—S.	↑ −30	−21 ↑	−21	−13
P.	8773 ↓	9830	11204 ↓	—

Negative polarisation is practically abolished by boiling temperature; on the other hand the resistance of the preparation is lessened, but not in the proportion which might be expected from a comparison of series 16 (Sect. 12).

19.

1. Torp. Fresh. L 27 mm. OC 0·0083. $2\frac{1}{2}$–'P.

CT 0″·0629.

L.—S.	↑ +163	−184 ↑	+45	−163 ↑	−20; +16	−41 +11	−135 ↑	−49 +2	−135
P.	543 ↓	390	465 ↓	407	457;	457 ↓	394	390 ↓	407

This series is interesting from the appearance of effects in both directions.

20.

1. Torp. Fresh. L 27 mm. OC 0·0105. $2\frac{1}{2}$–'P.

CT 0″·0629.

L.—S.	↑ +756	−470 ↑	+387	−384 ↑	+153	−322 ↑	+88	−337 ↑	+20
P.	548 ↓	332	527 ↓	382	631 ↓	390	519 ↓	448	423

The points of interest here are, first the powerful positive initial effect, and then the relation between homodromous and heterodromous current strengths in the primary circuit.

21.

With L and 21″.8 closing time the negative polarisation shot the scale out of the field in both directions. It was not worth while to record larger numbers than those in series 16.

22.

5. Torp. 2. Day. OC 0·0220.

Polarisation by a transversely directed polarising current.

	CT 0″·0764.					CT 1″·024.			
XX.—S.	−85 ←	−20 →	−10 ←	+25 →	−60 ←	−35 →	−54 ←	−38 →	−42 ←
P.	652	665	669	665	677	—	5465	5539	5560

The great strength of the polarising current arises from the shortness

and large sectional area of the path which it has to follow in the preparation when it is placed crosswise. In a transverse direction (except in the incomprehensible effect observed in exp. 4) there is no positive polarisation and only very weak negative polarisation.

23.

5. Torp. 2. Day. *OC* 0·0030.

Polarisation when the current is led in transversely.

CT 0″·0764.

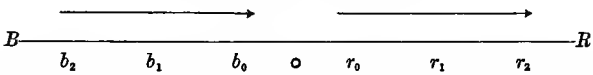
		r.	*b.*			*r.*	*b.*		
XX.—*S.*	↑	+190	−140	Led in transversely	↑	32	17	↑ 0	0
P.		134	75		↓	116	79	116 ↓	113

r and *b* signify red and black, the colours of the two halves of the scale, and consequently the direction in which the mirror was deflected. It is seen that under these circumstances there is scarcely any effect.

24.

5. Torp. Fresh.

Proof of the pile-like arrangement of the electromotive force in the polarised preparation of the organ.



B R represents schematically the preparation as a linear conductor, through which the shock of the organ current and the homodromous current pass from *B* to *R*. If positive and negative homodromous and negative heterodromous polarisation depend upon the pile-like arrangement of electromotive forces, then in every case polarisation must appear in the same direction between any two given points of the line *B R*, which would be of the same strength if the distance of the leading-off points is equal; and of greater strength if the distance is greater and the external resistance is sufficient. $B R = L$ amounted to 22 mm., $b_2 r_2$ 18 mm., $b_0 r_0$ 1·5 mm., $o b_2 = o r_2$ 9 mm., $b_1 r_1$ about the same. In order not to confuse the results, the positive organ-current force, although observed constantly in every part, has been left out of account.

A. Homodromous currents, absolutely and relatively positive polarisation.

		CT 0″·0764.					*CT* 0″·0764.							
	↑	$b\ r_2$	$b\ r_0$	$b_2\ r_2$	$b_0 r_0$	New preparation.	↑	$b_1\ r_1$	$b_0\ r_0$	$b_1\ b_2$	$r_1\ r_2$	$b_1\ b_2$	$b_2\ r_2$
XX.—*S.*		+205	+20	+146	+6			+500+*x*	+148	+170	+31; +12	?	+20
P.		171	163	159	159			213	180	167	159; 163	147	134

B. Homodromous current, absolutely and relatively negative polarisation.

CT 1″·024.

	$b_0 r_0$	$b_1 r_1$	$b_2 r_2$	$o\ b_2$	$o\ r_2$	$b_0 r_0$	$b_2 r_2$
XX.—*S.*	−64	−125	−160	−117	−121	−45	−145
P.	703	703	715	707	711	715	707

C. Heterodromous current, relatively negative, and absolutely positive polarisation.

		CT 0″·0764.								*CT* 1″·024.			
XX.—*S.*		$b_0 r_0$	$b_2 r_2$	$o b_2$	$o r_2$	$b_0 r_0$	$b_2 r_2$	New	$b_0 r_0$	$b_2 r_2$	$o r_2$	$b_2 r_2$
		−10	−105	−30	−45	−10	−47	prepa-	−78	−215	−70	−250
P.	↓	71	75	75	79	79	75	ration.	↓ 761	744	757	736

25.

5. Torp. Fresh.

The galvanometer circuit (*S*) forms a collateral closure to the preparation, as in Fig., 8, *A* and *B*, and p. 455.

		CT 0″·0764.								*CT* 1″·024.			
XX.—*S.*		230	↑ 150	216	↑ 158	193	↑ 162	190		255	↑ 245	255	↑ 255
P.	↓	141	269 ↓	145	239 ↓	146	228 ↓	146		↓ 1162	1254 ↓	1179	1267

Distance of bobbin from mirror of galvanometer,

21 cm. 36 cm.

Number of turns 5000.

XIII.

LIVING TORPEDOS IN BERLIN.

By E. du BOIS-REYMOND.

(Second Paper.)

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XIII[1].

1. Introduction.

During the past summer (1884) and this winter and spring (1884–5), through the kind co-operation of the Director of the Berlin Aquarium, Dr. Otto Hermes, I have again had at my disposal several living torpedos (*T. marmorata*) from Trieste. Those in the summer were four females, I, II, III, IV, and their respective lengths were 29·5, 35, 31·5, 31·5 cm. Torpedo I arrived on June 9th, in a very sickly condition. As I worked with it during the day its breathing was still regular, but it closed its spiracles only partially, and it was evidently in a sort of opisthotonus, so that its back was very concave in a sagittal direction. The torpedos II, III, IV arrived on June 23rd, and were killed on July 9th, July 16th, and August 13th respectively, after remaining for about 2, 3, 7 weeks in the tanks of the Berlin Aquarium. The winter supply which was brought on October 22nd consisted of three females, V, VI, VII, and their lengths were 28·5, 26·5, 28 cm. respectively; they were killed on the 21st and 30th December, 1884, and on the 6th May, 1885, after a period of about 8, 9, 28 weeks. An accident befell a first consignment in spring this year, but on May 8th a female (VIII), 34 cm. long, arrived in good condition, and was experimented with on June 3rd.

In the summer of 1883 I had also allowed three and five weeks to elapse after the arrival of fish before killing them, and in the winter of 1883–84 a period of ten and fifteen weeks. The reason of these delays is, that in order to make full use of a torpedo it is necessary to devote two whole consecutive days to the work without interruption, and my occupations only permitted this at wide intervals of time. I mention this because the functional activity of the fish naturally suffers very much from a prolonged

[1] See No. XII of this book.

captivity, especially during the summer. In the summer of 1883, when they reached here earlier, they had kept in comparatively good health. The fish of the spring consignment in 1884 remained indeed quiet, buried in the gravel—a position which they abandoned as soon as they became seriously ill (p. 419); they looked quite well, breathed regularly, and struggled vigorously when lifted up by the tail. But they gave shocks only after repeated violent stimulation, and their electrical force was so much lowered that on July 29th I did not succeed in making the shock of the fourth torpedo perceptible to my audience in the manner described in my former paper. The condition of the organ corresponded obviously to its impaired functional activity, just as is the case with frog preparations which do not react well[1]. The organ was soft, deliquescent, drops of liquid exuded from the cut surfaces, and as it had lost its plumpness the organ preparations could not be made so well as before. Its organ current appeared also less strong and showed peculiar irregularities (see below, § 2). The cause of this was undoubtedly that the fish fasted at a comparatively high temperature, but up to this time no mode of feeding them had been discovered (p. 419). The keepers fancied that the seventh torpedo, which had lived in the Aquarium the whole previous winter, more than half the year, had taken nourishment. They inferred this only from its apparently vigorous condition, but I found the stomach and intestine quite empty.

Fish kept in winter at only 10·5–12°C. certainly suffer less in confinement than summer fish. However, judging from their electrical functional activity, they also are far from the normal condition[2]. Even when put into warm sea-water but twenty-four hours before the experiments, they gave feeble shocks only, and only on strong excitation.

The field of our experiments on electrical fishes is much within the limit beyond which the greatest amount of functional activity becomes indispensable, and in spite of the bad condition of several preparations, I succeeded, as I believe, in attaining some not unimportant results. I purpose to communicate these now, without awaiting further consignments, as their safe arrival depends more or less upon chance. On the other hand, the deficiency of functional activity undoubtedly had for result, that certain other questions could not be completely settled. I will however speak

[1] Untersuchungen über thierische Elektricität, vol. ii. pt. i. p. 168.
[2] Comp. i. p. 121; Untersuchungen, etc., p. 266.

about these questions also, according to the position of the subject at the present moment, because the scantiness of material and the uncertainty of its condition compel me to deviate in this case from the rule which I always strove to observe in treating of muscles and nerves, viz. to publish investigations, only when they had been completed according to the best of my knowledge and power.

The preparations for the experiments were the same as in those of the first communication. The animals were killed in all cases in the way described there (p. 438), by punching out the electrical lobe of the brain with a single blow of a hammer. This operation presents no difficulty to any one who studies Savi's drawing[1] closely, even though he be not so conversant as Prof. Fritsch with the anatomy of the torpedo. It is advisable to make a slit in the sagittal plane in the skin first of all, as it easily slips laterally from under the borer and takes the rod with it, so that the sagittal plane does not divide the hole in half. The fish never gives a shock after removal of the lobes, even if this has not been accomplished faultlessly, but it can still wriggle for a long time as well as perform reflex movements. Any part of the organs not used on the day when the fish was killed was kept on ice in hot weather.

Perhaps it is not useless to remark that the polarisation reverser with its time disks[2] regulating the duration of a polarising current, which I have used for many years as well as in the present experiments, is to be found described and figured[3] in the concluding part of my 'Untersuchungen über thierische Elektricität' recently published. My investigations on polarisation at the junctions of dissimilar electrolytes and in the interior of moist, porous semi-conductors are also communicated there in full; these form one of the most important foundations for all researches on electromotive tissues, but until now only extracts had appeared in the first volume of the 'Gesammelte Abhandlungen.'

2. On the electromotive behaviour of the skin of Electrical Fishes.

I have sought in vain, in organ preparations of Malapterurus

[1] Matteucci, Traité des Phénomènes électro-physiologiques des Animaux. Paris, 1844, Planche I.

[2] Gesammelte Abhandlungen, etc., vol. i. pp. 3, 13, 34; vol. ii. p. 718.

[3] *Loc. cit.* vol. ii. Part ii. Berlin, G. Reimer, 1884, pp. 389–395, Plate vi. Figs. 151, 152, A, B. The means by which I can insure that a polarising or tetanising current shall last for small fractions of a second only, are not yet given here; this will be done at the first opportunity.

electricus for an electromotive action during rest, that is for an organ-current. This failure must seem strange now that such actions have been demonstrated[1] in the Gymnotus and Torpedo, and as it is alleged even in the imperfect electrical organ of the common skate. It can be explained, neither by the lowered functional activity of the preparations, for they were in much better condition than many preparations of the Torpedo which now gave me the organ-current, nor by the imperfection of the experimental method, for I made use of the nerve multiplier; and the resistance of the old conducting vessels and of the salt pads covered with thin films of white of egg was certainly less than that of the present unpolarisable apparatus. The polarisation of the platinum in the old conducting vessels is all that remains to explain that a constant weak action might escape me ; it did not, however, prevent my perceiving a slight positivity of the external surface of the skin in comparison with all other natural as well as artificial boundaries of the organ preparation, an action with which, as will now be shown, the organ-current if present would have been of the same order.

In the Gymnotus, Sachs found points of the skin feebly positive (0·0050 Daniell=0·0053 Raoult; see p. 440) in comparison with points of natural longitudinal section not covered with skin and situated in the same transverse plane, as also in comparison with such points of artificial longitudinal and transverse section. In comparison with the surface of that part of the organ turned towards the head, the skin is feebly positive, electrically the same, or very feebly negative ; and in comparison with the surface towards the tail, it is more strongly positive, as this gives the algebraical sum of the organ current of the length situated between the leading-off points, and of the skin current. In the first adjustment, for example, the force amounted to a mean value of 0·0040, in the second to 0·0195 ; whence by calculation the force of the skin current is found to be 0·0155/2=0·00775, and this approximates sufficiently to the direct measurement given above $(0{\cdot}005)^2$.

The question naturally forced itself upon me, how the skin behaves electromotively in regard to the interior of the organ in the Torpedo. The case is not so simple here as in Malapterurus which is not complicated by any perceptible organ-current, nor as in Gymnotus, where the organ is bounded laterally by skin,

[1] Untersuchungen, etc., p. 169 f.
[2] Untersuchungen, etc., p. 172.

and where consequently the organ-current can be excluded by leading off from skin and organ from points in a line which is isoelectrical as regards the shock and the organ current. In the torpedo the polar surfaces of the organ preparations are covered with skin, and if on the one hand, the leading-off is from one of these surfaces, on the other hand, from the lateral surface or from a transverse section of the preparation, the organ-current of the length of the columns included between the two leading-off points is always present in the circuit, and any possible electromotive actions of the skin can only be determined by elimination: this can, however, be accomplished in the following manner.

In Fig. 19 an organ preparation is represented: at V it is bounded by the ventral skin, and at D by the dorsal. The curves 1–6 represent different positions of the galvanometer circuit, the terminals of which are formed by the clay points of the unpolarisable conducting tubes, and in which equilibrium is maintained by the circular compensator for the purpose of measuring the electromotive forces. The point m divides the length of the preparation as nearly as possible in half; the points d', d_1 and v', v_1 lie as close as possible to the dorsal and ventral skin respectively[1].

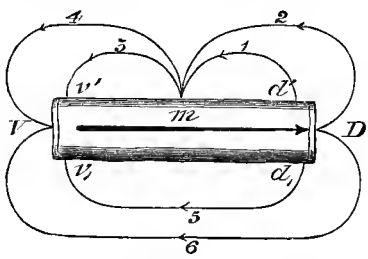


Fig. 19.

In all the cases, organ-current force is present in the circuit, and besides this, in the cases 2, 4, 6, any electromotive action of the skin that there may be. If the dorsal points are shifted from d', d_1 to D, or the ventral points from v', v_1 to V, then not only is the skin taken into the circuit, but also the tract of the columns between the points is slightly increased. If the skin is electromotively inactive, then the removal of d', d_1 to D as well as of v', v_1 to V must result in a slight strengthening of the positive organ-current force, and this must be the same in both cases if the preparation is of regular columnar arrangement, and if the additional-column tracts are the same length. On the other hand, a deviation from this

[1] The adjustments mV, mD had been investigated by Eckhard, who did not find electromotive action here any more than between V and D in the organ at rest. (Beiträge zur Anatomie und Physiologie, vol. i, Giessen, 1858, 4, pp. 161, 162. Comp. i. pp. 204, 210.)

behaviour under these circumstances is to be attributed to electromotive action of the skin.

Such a deviation in fact shows itself with great uniformity, so that on passing from 1 to 2 (from md' to mD) on the back, a considerable increase of the positive force, and on passing from 3 to 4 (from mv' to mV) on the belly, a less considerable weakening of the positive force is observed. The latter result cannot proceed from increased length of the column tract. On the other hand, both results are fully explained, by assuming that the skin is feebly positive in comparison with the interior. At first sight, one might be inclined to attribute the fact that the enfeeblement on the belly is less in amount than the increase in strength on the back, to different electromotive character of the pigmented skin of the back and of the pigmentless skin of the belly, which is however not demonstrable with certainty in the case of the frog[1]. Another ground of explanation, less remote, and which makes no fresh supposition necessary, is that the increase of strength of the organ-current, due to the greater length of the column tract between the points, adds itself to the skin action on the back and deducts itself from that on the belly.

The first experiments were made with the last summer fish (IV). In a successful experiment I obtained—

in the curve	1 (md')	.....	+	0·0057	Raoult.
,, ,,	2 (mD)	.....	+	0·0103	,,
,, ,,	3 (mv')	.....	+	0·0049	,,
		.....	+	0·0063	,,
		Mean	+	0·0056	,,
,, ,,	4 (mV)	.....	+	0·0034	,,
		.....	+	0·0029	,,
		Mean	+	0·0032	,,

Thus the increase in strength on the back at the removal of md' to mD amounted to 0·0046, the diminution in strength on the belly at the removal of mv' to mV, in accordance with what has been said above, amounted to only about the half, 0·0024. Let x be the difference of potential between the skin and the interior of the organ, δ the force of the column tract between the skin and the points lying next to it, then we have on the back.

$$0{\cdot}0057 + \delta + x = 0{\cdot}0103,$$

[1] Untersuchungen, etc., vol. ii. part ii. p. 14.

on the belly

$$0{\cdot}0056 + \delta - x = 0{\cdot}00315,$$

which gives

$$\delta = 0{\cdot}0011,\ x = 0{\cdot}0036.$$

When I wished to repeat the experiments last winter, on fish V, killed on December 21st, I came across a new kind of phenomenon of the organ current, viz. in several organ preparations I found it positive in the dorsal half agreeably to law, but on the other hand, contrary to law, negative in the ventral half of the columns. As the fish had been removed rapidly from the cold tank of the Aquarium to warmer water, a disturbance owing to hydrothermal currents at first occurred to me. But I was compelled to give up this idea, because fish VI, which I killed on December 30th, after I had kept it for more than twenty-four hours in water at 17·5°, exhibited the same phenomena, only with the difference, that this time the dorsal half of the columns acted negatively. I now proceeded to make measurements again, and obtained—

in the curve	1	(md')	− 0·0021	Raoult.
„ „	2	(mD)	− 0·0012	„
„ „	3	(mv')	+ 0·0067	„
„ „	4	(mV)	+ 0·0057	„
„ „	5	($v_1 d_1$)	+ 0·0029	„
„ „	6	(VD)	+ 0·0029	„

The first thing to be remarked is, that as in the first series and in this, $mV < mv'$, but in this series it happened that $mD < md'$, for now the skin current force is deducted from the organ current force on the back also; further, that the force in curves 5 and 6 by reason of the opposite action of the two halves of the columns, was less than that of the stronger half, even if $v_1\ d_1$ ought to have been somewhat $<$, and VD somewhat $> 0{\cdot}0045$, instead of both amounting to only 0·0029 without perceptible difference between them.

In order to determine x from our numbers, we must not proceed as above, where we could assume that δ, which represents the increase of organ current consequent on the lengthening of the column tracts in the transition from md' to mD, and mv' to mV, on account of the sensibly equal activity of both halves of the columns, is the same at the belly and the back. But if we assume that the one entire half of the columns acted positively, the other entire half negatively, then we can proceed in the following way.

Let δ_d denote the increase at the back, δ_v that at the belly, then

in order to determine the values of x, δ_d, δ_v, we have the three equations,

$$-0{\cdot}0021-\delta_d+x=-0{\cdot}0012,$$
$$+0{\cdot}0067+\delta_v-x=+0{\cdot}0057,$$
$$\delta_v=-\delta_d\tfrac{67}{21},$$

whence we have

$$\delta_d=0{\cdot}00024,\ \delta_v=0{\cdot}00131,$$

and according as x is calculated from the first or the second of the equations containing it, and which do not agree exactly with each other on account of errors of observation,

$$x=0{\cdot}000924 \text{ or } =0{\cdot}000869, \text{ mean } =0{\cdot}000896.$$

It would have been scarcely practicable to give more exact values of the ratio of the lengths of the positively and negatively acting segments of the columns; at any rate, the attainment of better numbers, if it is worth the trouble, must be reserved for the future. In the mean time, it seems as though the electromotive force of the skin is considerably less in the winter fish (about four times) than in the summer fish; this is very possible.

Thus the skin of the torpedo behaves electromotively like that of the gymnotus, in regard to the direction as well as to the magnitude of the action, and certainly like that of malapterurus in regard to direction; the force is probably here much the same in amount as in the two other fishes (see above, p. 482). Three modes of explaining this action offer themselves.

The first question to occur is, whether it does not denote a difference of potential between the longitudinal and transverse section of the columns, for perhaps the skin may play the part of an inactive conducting covering over the natural transverse section of the columns, like the tendinous expansions over natural transverse section of muscle. This idea is negatived, because no action is perceived between the lateral surfaces of the columns and an artificial transverse section, and there is no perceptible change in the organ current, on moving a clay point which is near a transverse section, to the transverse section itself.

The second hypothesis is, that in the case of the gymnotus, the skin forms with the material for leading-off and the organ, a liquid battery in the following way[1],—

Physiological Clay | Organ + Organ | Skin + Skin wetted with river water | Clay;

[1] Gesammelte Abhandlungen, etc., vol. ii. p. 265.

in the case of the torpedo,—

Physiological Clay | Organ + Organ | Skin + Skin wetted with sea water | Clay,

and in the case of the malapterurus,—

White of egg | Organ + Organ | Skin + Skin wetted with river water | White of egg.

It may seem surprising that the interposition of sea water, and still more of white of egg with alkaline reaction, instead of the clay kneaded up with physiological solution of chloride of sodium, does not cause a more considerable difference of action. In order to judge certainly as to this, it would be necessary to study first the chemical reaction of the torpedo's skin, and also to make experiments with conducting liquids of a more decided electro-chemical character.

The third hypothesis is, that the skin possesses its own independent electromotive action, like the skin of the naked amphibia, according to my discovery[1]. This assumption has also much against it. In the first place, the direction of the force would be the opposite, inasmuch as the action of the skin is from without inwards in the amphibia. Secondly, it would be more than eleven times less than in the case just mentioned, where the skin current force is found to be comparable to that of muscle and nerve[2]. Thirdly, up to the present time, skin currents have been observed in none of the fishes investigated, including those without scales, like the eel[3]. Fourthly, the electromotive activity of the skin seemed to me to outlast that of the organ in the torpedo, and this would be more in accordance with a liquid battery. Fifthly, I did not succeed in observing an electromotive action of determined direction and amount between the external and internal surfaces of a detached piece of skin. I employed the same method in these experiments as Rosenthal for the skin of the frog[4]. I made openings with the punch in two mica plates laid one over the other, placed the skin between them, and pressed the mica plates between the clay shields of the leading-in pads, so that on the one side only the ventral surface of the skin, and on the other side only its dorsal surface

[1] Monatsberichte der Akademie, 1851, p. 380. Untersuchungen, vol. ii. part ii. p. 9 f.

[2] Gesammelte Abhandlungen, etc., vol. ii. p. 261.

[3] Untersuchungen, *loc. cit.* pp. 16, 17.

[4] Archiv für Anatomie, Physiologie, etc., 1865, p. 309.

touched the clay. It should be mentioned that in these experiments the skin was no longer fresh, and might have suffered by dryness as well as from frequent handling of the fish. The result however, in conjunction with the other reasons, tells strongly against independent electromotive action of the skin.

Experiments like those by which I determined the electromotive action of the skin of the frog[1] would be necessary, in order to decide between the second and third hypotheses. Unfortunately, there are here great difficulties. The detachment of sufficiently large pieces of uninjured skin, which is facilitated in the frog by the lymph spaces lying underneath the skin, can scarcely be carried out in the torpedo. I tried therefore to observe currents in the two first winter fishes (V and VI), by placing on them, not simultaneously, pads soaked in solution of sodium chloride. In the frog and other naked amphibia, a strong current is always obtained in this way from the more recent to the earlier points of contact, because by the caustic action on the skin, the electromotive force, the direction of which is from the exterior to the interior, is diminished, or even annihilated. I made the experiments on the tail of the Torpedo, having amputated it high up along with a piece of the vertebral column and a slice of the body. Naturally, currents were not wanting, but they had sometimes one, sometimes the other direction, and more often, they did not disappear on a prolonged application of the pads, so that no importance can be attached to them; all the less because there was a danger of illusive effects, partly arising from the interior of the preparation, partly from the neighbouring cut surfaces. A comparison of the strengths of the currents with those in the frog would have had no meaning; measurements of force are precluded by the transitoriness of the actions.

The whole matter is not very important, and has hardly any relation to the electromotive property of the organ of the Torpedo and of the Gymnotus. It is much rather to be supposed that in other fishes also, the skin is feebly positive to internal parts which are without electromotive action. In them, however, parts are wanting, which, like the organ preparations, consist only of skin and a tissue which is inactive or possesses only feeble electromotive action, in accordance with known laws. Whether the observed positivity of the skin in the Malapterurus may possibly contribute anything in support of Prof. Fritsch's hypothesis, according to which, the organ of this fish has its origin in the mucus cells

[1] Untersuchungen, *loc. cit.*

of the skin [1], must remain undecided. In any case, the examination of dissimilarities in the skin forms an essential part of the investigation of the organ current, and the possibility of separating these two actions from each other, testifies at least to the superiority of our experimental methods, for until recently the existence of any action was regarded as doubtful and even denied.

3. On Polarisation of the organ by alternating Currents.

The most important questions in regard to the electrical organ, are for the moment closely connected with its behaviour when homodromous or heterodromous currents are sent through it, first those which concern the polarisations which they leave behind them, secondly, those which concern the apparently irreciprocal conduction of the organ. Is there any relatively positive polarisation of the organ, or is it nothing but the after-effect of a shock which gradually loses itself in the organ current? Does the organ conduct irreciprocally, or does only the semblance of such conduction arise, owing to absolutely positive polarisation adding itself to the homodromous current, whatever may be its cause and significance?

In order to decide the first question, I had at an earlier date tetanised organ preparations, supposing that if the absolutely positive polarisation were the after-effect of the shock, it must appear with greater strength after a short tetanus. I made use of the sliding inductorium with the ordinary arrangement, and its secondary coil was pushed quite up to the primary coil, and the latter filled with wires. The terminals of the secondary coil were connected with the two binding screws of the switch which are connected usually with the terminals of the battery circuit [2]. The spring of the inductorium vibrated, and as soon as the switch had opened the galvanometer circuit and closed the secondary circuit, each in two places, the induced currents reached the preparation. On the falling back of the switch, I expected very strong absolutely positive polarisation in any case, but after tetanising during $5''$, I obtained only feeble polarisation in a direction as if opening shocks alone were present, viz. absolutely and relatively positive polarisation with homodromous, absolutely positive and relatively negative polarisation with heterodromous opening shocks [3].

[1] Monatsberichte, etc., 1881, p. 1154. Archiv für Physiologie, etc., 1882, p. 66.

[2] In Fig. 151, Plate vi. of vol. ii. part ii. of the Untersuchungen, they are the screws with which wires s_1 and s_4 are connected.

[3] Comp. p. 461. Here, by a slip of the pen [corrected in the translation], the word primary was used instead of secondary. The mode of producing a tetanus of determined

The result could not be considered decisive, because the experiments were made in the winter 1883–4 with the last fish and on the second day, when the organ had no longer its full functional activity, and for this very reason, they could not be repeated at that time.

I resumed the thread of this investigation at the first opportunity, when I received a fresh supply of Torpedos in the following summer. The preparations employed in the following experiments were still not all that could be desired, for they were taken from the first fish which came to hand and which was in a state of opisthotonus (see above, p. 479), and again, 24–27 hours had elapsed since death; they still gave however a strong organ current, an infallible sign that their functional activity was maintained.

In order to work under simpler conditions, I began by substituting Helmholtz' arrangement of the inductorium for the usual one. I did not however obtain closing and opening shocks which were as congruent with each other as I desired, for if great exactitude is required, this is not so easy in practice as in theory. For reasons which may be deduced from my formulas[1], the closing discharge was now the shorter and stronger, while the opening discharge was the longer and weaker. In accordance with this, the closing discharge now played the same part as the opening one had done before: if it was homodromous, then after tetanus of 5″ there ensued strong absolutely and relatively positive polarisation; if it was heterodromous, feeble absolutely positive, relatively negative polarisation. The former action diminished very rapidly on frequent change of direction.

But now I replaced the inductorium by Saxton's machine, which I have frequently mentioned and most recently in the treatise on Secondary Electromotive Phenomena (see No. V). This instrument was constructed by Oertling for Dove, and I acquired it for the physiological institute at the sale of his effects after his death[2]. The turn-table was removed from the machine, and its axis was connected by a pulley with the spindle of a water-motor, which turned the armature seven times a second. The pachytrope[3] stood

duration by means of the switch, employed on a former occasion (see No. V of this work, par. x), was excluded here, as is self-evident, because the secondary coil would have furnished a derivation to the galvanometer.

[1] Gesammelte Abhandlungen, etc., vol. i. p. 233 f.

[2] Sitzungsberichte, 1883, vol. i. p. 360.

[3] [The pachytrope is a contrivance, by which the coils of wire surrounding the two legs of the armature can be connected in two ways, either so that the one is a continuation of the other and they are equivalent to one wire of double length, or so

at 'physiological.' With the springs 1 and 2 on roller I, 9 on roller II, every revolution between uprights C and D^1 gave two equal and opposite extra currents of unbearable strength when tested subjectively by the handles. The switch was connected with the terminals of the coils of the machine, instead of with the terminals of the induced circuit of the inductorium. As the switch performed its to and fro motion whilst the machine was working, the polarising effect of a series of really congruent alternating currents on the organ could be studied. Although the action of the machine at a distance upon the galvanometer could not be affected by the movement of the switch, inasmuch as the armature was constantly rotating, special care was taken to ascertain that no change actually took place.

I employed the 1″— and the 2″— disk of the polarisation switch in succession, and I also tetanised for 30″, 45″, 120″ by the watch. The result was very uniform. Whether the terminals of the rotating coils were connected with the dorsal or ventral surface of the preparations, and whatever might be the duration of the tetanus in fresh preparations, I could detect nothing but absolutely positive polarisation, of such strength that with 5,000 turns at a distance of 30 mm. from the magnet, and with $\epsilon = n$, the scale disappeared from the field of view. It then became more and more feeble, so that with some preparations the action was very weak even from the first. Never was it absolutely negative. The only difference, which seemed to follow on longer duration of the tetanus, was in regard of the persistence of the homodromous polarisation. It disappeared the more quickly as the tetanising was continued for a longer time.

It was astonishing how the organ preparations sustained such powerful shocks, for no arrangement was made for their gradation; it seemed as if they were accustomed, in virtue of their function, to impart such shocks to themselves.

It is not difficult to understand the results on tetanising with congruent alternating currents. First it is clear, that, as soon as congruent shocks succeed each other in alternating direction and at equal intervals, the reversal of the connections of the machine with the preparations is illusory, and in truth produces no change. In both arrangements, one is concerned with a similarly constituted

that both their similar ends are connected together, and they then form a wire of double thickness and half length. In the former case, the physiological effects are the stronger, and the pachytrope is then said to be 'at physiological.'—Tr.]

[1] Comp. the drawing in Poggendorff's Annalen, etc., 1842, vol. lvi. Plate ii. Fig. 1.

series of alternating homodromous and heterodromous currents. It is a matter of indifference for the preparation, whether the homodromous currents are produced with a position of the armature in azimuth 90°, and the heterodromous with that in azimuth 270°, or vice versa. According to our hypotheses, the homodromous and heterodromous currents produce equally strong relatively negative polarisation, and these polarisations, which moreover on account of the brief duration of the shocks attain no great extent, cancel each other. But besides the relatively negative polarisation, the homodromous currents produce absolutely and relatively positive polarisation, while according to our hypotheses the heterodromous produce no relatively positive, absolutely negative polarisation or only a trace, so that under favourable circumstances, the absolutely positive polarisation due to the homodromous currents makes its appearance in great force almost or entirely unmixed. The only point which remains obscure, is on what the more rapid falling of the homodromous polarisation after longer tetanising with congruent alternating currents depends.

4. An attempt is made to compare the negative polarisation due to the closing shocks of an inductorium by themselves, with that due to the opening shocks by themselves.

In order to judge of the secondary electromotive phenomena in the electrical organ produced by incongruent alternating currents, it is expedient to answer first the question, which of the currents, due to the same amount of electricity equalizing itself, give the strongest negative polarisation, whether the longer feebler closing shocks, or the shorter stronger opening shocks? This question must permit of a decided answer, by exposing an organ preparation in heterodromous direction to a series of closing shocks of the inductorium and to one of opening shocks alternately. In connexion with this subject, I remarked that in my experiments on internal polarisation of moist, porous conductors in general, I had neglected to perform this experiment, apparently so simple and yet so instructive; and I therefore determined to fill up this gap immediately. This seemed easy of accomplishment with the aid of Dove's disjunctor.

This apparatus, which after his death also passed into the possession of the physiological institute[1], consists of three pairs of copper wheels on a common glass axis, by rotation on which, they

[1] I had once before worked with the same apparatus, through the kindness of Dove, for a similar object. Untersuchungen, etc., vol. ii. part i. 1849, p. 405.

can be set at different positions in relation to each other. The two wheels of each pair are electrically connected with each other; the three pairs which may be denoted by *A*, *B*, *C* are insulated from each other by the axis. One wheel of each pair is constantly immersed by its amalgamated rim in a mercury trough. The rim of the other has eight copper and eight glass sectors of equal length, and a copper spring presses on its circumference.

One pair, *A*, is made to close and interrupt the primary circuit. Another pair, *B*, is included in the secondary circuit, and it is placed by the breadth of a half-sector in such a position in regard to *A*, that its spring is against the glass when that of *A* comes to the glass; in this way the series of closing shocks alone is transmitted. If, however, *C* is placed in regard to *A* by the breadth of a half-sector, so that its spring rests upon glass when that of *A* comes to the metal, then only the series of opening shocks is transmitted. The same end may be attained in a simpler way, by using only one of the pairs *B* or *C* in addition to *A*, and setting the wheels first in one direction, and then in the other.

In my experiments the machine was driven by a water-motor, the axis of which was connected to the axis of the disjunctor by a pulley. The change in direction of turning was accomplished by crossing or not crossing the cord. The distance of the disjunctor from the water-motor was so considerable, that the crossing of the cord produced no perceptible difference in its tension. The number of shocks was 44 per second.

The separation of the one series of shocks from the other is indeed effected with the same degree of certainty only in so far as the continuous contact of the spring in its passage can be relied upon. This however seemed sufficient. For when opening shocks were excluded, and by holding handles, I placed myself in the circuit of the secondary coil and brought it to within one or two centimeters of the primary, the sensation I experienced was quite uniform; if, however, the spring closing the primary circuit had jumped, each opening would have been perceived by me as a violent shock.

By these means I hoped to learn how the internal polarisation of moist porous bodies and the negative polarisation of the electrical organ, most nearly comparable with it, and perhaps also that of muscles and nerves, depends upon the time occupied in equalisation, when the amount of electricity is constant. The polarisation switch was put into the secondary circuit, and the series of shocks of 5″ duration was led through the usual conducting vessels pro-

vided with clay shields, to the object to be polarised. Blotting-paper pads, white beech wood, pumice-stone, roofing tiles were made into bars 50 mm. long and one square centimeter in transverse section, and served for such objects. The blotting-paper was soaked with distilled water, and the wood, pumice-stone and tiles were boiled in it until they sank below the surface[1]. In the same circuit, secondary in regard to the induction, primary to the polarisation, was placed the galvanometer P with 53 turns of wire at a distance of 20 mm. from the mirror.

A second pair of conducting vessels with wedge-shaped pads, the edges of which, protected with physiological clay, were laid on the object to be polarised, formed as usual the terminals of the galvanometer S.

At first it seemed that the negatively polarising effect of the closing shocks exceeded that of the opening shocks. It was however soon proved that this could not be relied on. If the experiments went right, the deflection of the galvanometer P, due to the closing shocks, ought to have been sensibly equal to that due to the opening shocks. But it was observed that the closing shocks always produced by far the greater deflections. As at first I employed ordinary inductoria, in which no special measures are adopted for the insulation of the turns of the wire from each other in the secondary coils, I supposed that a channel for sparks had formed itself in the interior of the coils, in which the high tension electricity due to the opening induction, sprang over, instead of making its way through the object to be polarised and the galvanometer P. In order to work under simpler conditions, I abandoned the polarisation object and the conducting vessels in connexion with it, and replaced them by one or two resistance coils out of a plug rheostat, which gave a resistance of 60 and 120 Siemens units, respectively. Instead of the ordinary induction apparatus, I took a Ruhmkorff inductorium by Siemens and Halske, and as its shocks, even with only two Bunsen chromic acid cells in the primary circuit, seemed likely to damage the galvanometer, I drew the primary coil somewhat out of the secondary, so that I gradually lessened the effect as in the ordinary inductorium. In this apparatus, it is certain that no sparks sprang over in the interior of the secondary coil; but, on the other hand, it was very difficult to put a stop to all sparks and lateral discharges owing to the length of the conducting wire, which was necessary

[1] Comp. Untersuchungen, vol. ii. part ii. p. 430 f.

in order that the actions at a distance of the inductorium on the galvanometers should disappear. This aim seemed to be sufficiently attained when all the conducting wires were thick and covered with guttapercha. But here also, the opening shocks proved much weaker in their effect on the galvanometer *P* than the closing shocks, and the difference was so much the greater as the primary coil was pushed into the secondary; with a certain strength of the induction indeed, the effect of the opening shock disappeared, and beyond that it was reversed, so that the mirror was deflected in the same direction by it as by the closing shocks, only much more feebly and very irregularly.

I now suspected that sparks sprang over in the galvanometer coil itself, although I did not understand how inverse deflections should result. However, in order to proceed quite surely, I replaced the usual high resistance bobbin of the galvanometer by a similar one wound with wire covered with guttapercha, but the result remained the very same; afterwards, just as before, the series of opening shocks produced an infinitely small deflection in comparison with that due to the closing shocks, and with a greater strength of induction, the former deflection was inverted, i.e. the opening shocks acted apparently in the same direction as the closing shocks. That the opening induction continued in full force, was proved by sparks at every interruption at any part, and by lateral discharges when opportunity offered at any exposed part of the circuit.

Single closing and opening discharges, produced in the primary circuit by means of a key while the disjunctor remained at rest, effected quite regular deflections equal in amount on both sides of the zero point; but the most remarkable fact was, that when Wagner's hammer or Foucault's mercury interrupter was put in the primary circuit instead of the disjunctor, the closing and opening shocks maintained equilibrium as perfectly as was expected.

As the mirror was now observed to vibrate in time with the interruptions, the suspicion arose that the disappearance of the effect produced by the opening discharges on the mirror, might be connected with the greater number of interruptions which occurred in using the disjunctor, owing to its being turned by the water-motor. I therefore directed an assistant to turn the disjunctor first slowly, then more and more quickly by means of the pulley connected with it: this proved that in fact the opening shocks

acted regularly with slow turning, but more and more feebly with more rapid turning, until their effect was reversed. If it was arranged that both shocks passed, the closing shocks always preponderated, all the more as the turning was more rapid.

The only question now left was, whether the irregularity which ensued on turning the disjunctor with greater rapidity, was peculiar to this apparatus, or whether it would be found also with a more rapid succession of closing and opening, than can be obtained by the use of Wagner's hammer or Foucault's interrupter. I put into the primary circuit of Ruhmkorff's inductorium, the interrupting spring of an ordinary inductorium which opens the circuit 150–300 times per second, according to a previous determination made by Helmholtz, and further a *C* tuning-fork interrupter by König of Paris, which performs 256 single vibrations per second, or opens the circuit 128 times. But I obtained regular actions with these means also, as well as with Wagner's hammer and with Foucault's interrupter, although the succession of the closing and opening shocks was much more rapid than with the disjunctor, which gave at most 45 opening shocks per second (see above, p. 493).

Thus it was proved that in consequence of an unexplained condition, the disjunctor is unable to give series of exclusively closing or of exclusively opening shocks, in which the same quantity of electricity equalizes itself, beyond a certain speed which is difficult to determine. The next problem would be to search out that condition, and to discover what becomes of the large amounts of electricity set in motion at high tension in the opening shocks of the inductorium, and which seem to disappear and leave no trace. It is essential to ascertain this in order to obtain a basis for the theory and construction of so important an apparatus as the disjunctor; for this reason, I did not feel justified in withholding this series of experiments although their result is not gratifying.

It may perhaps be asked, why after failing with the disjunctor, I did not attempt to compare the negative polarisation due to a single closing and opening shock, which, as the above and other observations show, can be obtained. This scheme naturally suggests itself, and I intend to revert to it. It will, however, not be at all easy to ensure the closure of the galvanometer circuit at the same time after the polarising shock in the two cases. The end may also be attained by a slowly turned disjunctor, but not without further provision for regulating the number of the shocks which reach the polarisation object. It will be as necessary, as in

the case of single shocks, to arrange for a uniform closure of the galvanometer circuit after each individual shock.

All this demands a special investigation, for which I have not leisure at present. In regard to the question how the negative polarisation in the electrical organ behaves for closing and opening shocks, we must be content with the simplest assumption in the mean time, viz. that it is proportional to the amount of electricity, and thus is the same for the two shocks.

5. Continued discussion of the results of polarisation of the organ by alternating currents.

The result of polarising the organ by the alternating currents of induction apparatus, can be readily explained by means of the last-mentioned hypothesis in conjunction with the indubitable fact, that when the direction is homodromous, strong currents of short duration produce stronger absolutely and relatively positive polarisation than weaker currents of long duration. For here also, as with the congruent alternating currents of Saxton's machine, the relatively negative polarisations in both directions cancel each other: since the heterodromous shocks produce no relatively positive polarisation or only infinitely little, the homodromous absolutely positive polarisations alone remain, and these prove to be stronger with homodromous strong shocks of short duration than with homodromous weak shocks of long duration.

It is another question, how much these experiments have contributed to decide whether the homodromous absolutely positive polarisation is only an after-effect of a shock, or an independent phenomenon. This decision is not such as I had expected. I had overlooked the circumstance that the relatively negative polarisations due to both currents may cancel each other, but not, as I had assumed, the relatively positive ones, because, if there are any such at all in the organ, the heterodromous current does not produce them, or only produces traces of them. Thus it was an error, when I supposed, that tetanising in itself would leave behind it no polarisation, so that an absolutely positive effect produced by it must be conceived of as solely an after-effect of shocks. If the observed results have any bearing on our question, it is rather in the opposite sense. It has been seen that, to express myself briefly, according to the polarisation theory the phenomena are not difficult to explain; whereas the after-effect theory fails to explain on what the weak absolutely positive polarisation with heterodromous direction of the stronger

shocks of short duration depends. For it is difficult to imagine that when a shock is once discharged, it will not reach a height corresponding to the functional activity of the organ, independently of the strength of the excitation; and it seems just as little probable, that the negative polarisation due to short sharp shocks, should exceed that due to long feeble ones. According to the analogy of the polarisation of metal electrodes, the opposite would rather be expected. This is the point in respect of which the experimental basis sought for in vain in the previous paragraphs, is necessary.

6. Unsuccessful experiments to produce relatively positive polarisation by heterodromous currents.

As I reflected upon these questions it occurred to me, that I had not followed a certain path of experiment to its utmost limit, even though I had not left it quite untrodden, and that it might possibly lead to the goal. We have indeed laid down as a fact founded on experience, that relatively positive polarisation due to the heterodromous current, was never observed in the experiments with battery currents on the Malapterurus, Gymnotus and Torpedo; but we have not hitherto undertaken experiments for the express purpose. Such experiments must be designed so as to act on organ preparations by heterodromous shocks as strong, and at the same time of as short duration, as possible. If we should succeed in observing in this way relatively positive, absolutely negative polarisation, there could be no longer any doubt as to its existence, for there is no reason to assume reversal of the direction of shock of the organ.

At first, I still adhered to the use of galvanic currents closed for a short time. I had indeed at an earlier date (see p. 473, Series 19 and 20) sent the current of 50 Groves through organ preparations for a short time in vain; more often on the contrary, when the direction was homodromous, a negative preliminary shock had shown itself, which it was very difficult to interpret. The period of closing was 0″·0629; I now chose a period twenty times shorter.

4. Torp. Fresh. $OC + 0{\cdot}0078$.
CT 0″·00315.

L.—*S.*	−54;	−35	↑	+45;	+15	↓	−14
P.	↓ 13·5;	13		21;	20·5		15

The failure could not be plainer. I now placed my hope on induction shocks.

The Saxton's machine employed before, offered facility for such experiments. It has a pair of T-shaped springs previously de-

scribed. These springs change the alternating currents of the machine into currents which are all in the same direction, so that seven revolutions per second gave fourteen extra currents in the same direction. Whilst the machine was in motion, its circuit was closed for a shorter or longer period (0″·031, 0″·098, 1″·024) through the organ preparation. When the time of closing was only 0″·031, it depended on chance whether an extra current took place exactly in this period, but when it was 0″·098, one current must certainly come into action, and two currents might do so. The experiments were made this winter on the fifth fish on the second day, and on the sixth fish in a comparatively fresh condition. The organ preparations showed mostly reversed organ current between the ventral and dorsal skin; they were taken from the same organs as those preparations of which the one half acted negatively and the other positively (see above, p. 485). The result of the experiments was very unsatisfactory. There was often no action, as was to be expected with the very short period of closing. With homodromous direction of the currents, there was absolutely and relatively positive weak polarisation, and with heterodromous direction, there was much stronger absolutely positive, relatively negative polarisation. Example:—

6. Torp. Fresh. $OC - 0.0027$. $2' - P$.
CT 0″·031. CT 1″·024.
$\downarrow -220 \uparrow +18 \downarrow -210 \uparrow +60 \parallel \downarrow -430 \uparrow ?;\ +10 \downarrow -295$.

The primary current was not observed.

The Saxton machine was succeeded by an ordinary inductorium of a larger kind, and a battery of two large Bunsen chromic acid cells was put into its primary circuit. The spring of the Wagner hammer was removed, and was replaced by the disjunctor described above. This was arranged so as to allow only the opening shocks to pass, but of these, it gave thirty-seven in one second, of which therefore one or two passed the switch in 0″·031. As far as could be judged from the tension in the secondary circuit, the single shocks by far exceeded those of the Saxton machine. The result was essentially the same, no relatively positive heterodromous polarisation appeared.

6. Torp. Fresh. $OC + 0.0065$.
CT 0″·0031.
$\downarrow -500 + x; -370 \uparrow -155; +355$.

In the last case, presumably, two shocks passed through. I remarked as yet in these experiments, nothing of the disturbances

which I observed in a later series of experiments in using the disjunctor arranged for opening shocks alone, described above in § 4. But in any case, they would not explain the negative result obtained here.

I was unwilling to accept this rebuff, and determined to try further the effect of a single opening shock of Ruhmkorff's inductorium at its full strength. The polarisation switch would not answer this purpose, but a special switch had to be constructed, which rendered it possible to open the secondary circuit (which would otherwise have short-circuited the galvanometer) immediately after the opening of the primary circuit and the passage of the shock through the organ preparation, and then to close the galvanometer circuit. If the ordinary arrangement had been adopted, lateral discharges might have spread from the wedge-pads placed on the preparation, over the conducting vessels and beyond, and might possibly have left disturbing polarisations. On this account, I did not venture to adopt the plan of closing the galvanometer circuit at two places situated between the conducting vessels and the galvanometer, but I arranged that the clay points of two non-polarisable conducting tubes connected with the galvanometer, should be so placed on the preparation, as to take up the polarisation current by the same movement which opened first the primary, and then the secondary current.

Four corks are fixed upon a glass axis, which can be rotated horizontally in wood bearings. Cork I carries a bent bar of copper, which at the initial position of the switch, by dipping into two mercury cups, closes the primary circuit of the inductorium, in which three large Bunsen cells are included. Each of the corks II and III carries a non-polarisable conducting tube, the clay point of which in the first instance is suspended above the organ preparation. Cork IV carries a copper hook, one end of which is the terminal of the secondary coil and dips into a mercury cup. Its other end is connected with the other terminal of the coil permanently, but is movable. When the glass axis is turned from its initial position, the primary circuit opens, whilst the secondary is still closed. The shock passes through the preparation, to which it is led by amalgamated zinc plates in solution of zinc sulphate, and by zinc pads protected by clay shields. Immediately after, the secondary circuit opens, and thereupon the clay points touch the preparation. Two marks are made on the milled edge of the wood disk which serves to turn the axis, of which one shows the

initial position of the switch, and the other, that position at which the clay points just touch the preparation.

I convinced myself of course beforehand, that the passage of the shock would not produce any perceptible effect on the galvanometer, by using a clay model in place of the preparation; only a trace of negative polarisation could be perceived in the clay. I then compensated any organ current which might appear when the points were placed on the actual preparation, so that no deflection of any importance ensued when the points were replaced after they had been removed. The sparks in the primary circuit were diminished by Fizeau's condensator. The conducting wires of the secondary coil and beyond it consisted of wires covered with gutta-percha throughout. The number of turns was 5000, and the distance from the galvanometer was zero.

In spite of the risks connected with such considerable movements of electricity in the neighbourhood of a sensitive galvanometer, the experiment proceeded without any disturbance. It was made first on the torpedo which had been kept in the aquarium since October. It gave shocks only when it was strongly excited. But the preparations still showed an adequate organ current. The result of the experiment was again negative. I did not succeed in obtaining relatively positive polarisation by the heterodromous opening shock of the inductorium, the observed polarisation being relatively negative, absolutely positive. But since the homodromous shock only gave weak and relatively negative polarisation, it was evident that the functional activity of the organ was not sufficiently good for the purpose, and that the experiment ought to be repeated with a fresh fish.

This was effected a short time afterwards with the eighth torpedo, which arrived only in the spring, and which was in a comparatively good condition. But the result remained essentially the same. The homodromous shock now produced absolutely and relatively positive polarisation far beyond the limits of the scale, and the heterodromous absolutely positive, relatively negative polarisation extending also beyond the limits; effects in the same direction which disappeared very gradually were left behind. In the same measure as the functional activity decreased on more frequent repetition of the experiment, the intensity of the phenomena also diminished, until the ordinary type returned, viz. absolutely and relatively positive deflections due to the homodromous induction currents, and relatively negative, absolutely positive deflections due

to the heterodromous induction currents. For instance, I obtained with 5000 turns at a distance of 20 mm.

$$\downarrow - 85 \uparrow + 360 \downarrow - 57 \uparrow + 135.$$

But the heterodromous shocks never produced relatively positive polarisation.

There was still the possibility that the latter although present, might be masked by relatively negative polarisation. Although the opening shocks of the inductorium, by using the condensator are only of very short duration, I wished also to employ Leyden jar discharges, so that I should have left nothing untried. The same switch served for this as for the Ruhmkorff's opening shocks. In the first series of experiments on the same seventh Torpedo, Prof. Christiani discharged the jar, charged by Holtz' machine, through the preparation, and I put the clay shields in contact with it as soon as I had heard the sparks. The preparations were perhaps accidentally better than those which had been exposed to the induction shocks; for instance, we obtained

$$\downarrow - 448 \uparrow + 55 \downarrow - 11 \uparrow + 48.$$

It was however clear, that the experiments must be repeated with a fish with greater functional activity.

These latter and also the renewed experiments with the inductorium were performed on the eighth torpedo, which had just been killed. The following contrivance was now adopted. A fifth cork at the free end of the glass axis of the switch, carried a strong brass wire bent at right angles, one leg of which formed a prolongation of the axis, and was connected with an amalgamated zinc plate which was to conduct the shock to the organ preparation. The other leg, perpendicular to the axis, terminated in a closed ring. The charged jar was disposed so that its outer coating was connected with the other zinc plate. On turning the axis between the marks on the middle edge of the disk, the ring came so near the knob of the inner coating, that the spark sprang over and led the shock to the preparation a short time before the clay points reached it. In this series of experiments, the Leyden jar (with a coating of 565 square centimeters) was charged at the conductor of an ordinary electrical machine, for by regulating the number of revolutions of the disk, a greater uniformity and a more certain gradation of charge was ensured than in charging with the influence machine.

The experiments succeeded extremely well, without however

yielding the result sought for. At first, I charged the jar as strongly as possible, with fifty revolutions of the disk, and the polarisations produced by the discharge—absolutely and relatively positive by the homodromous, absolutely positive and relatively negative by the heterodromous shock—attained an indescribable intensity: many minutes passed before the end of the scale appeared again in the field of view. Then I decreased the number to five revolutions, to two, and even to one, yet still the comparatively weak shocks were followed by polarisations of great strength and perfect uniformity. For example, I obtained with five revolutions,

$$\uparrow + 270 \downarrow - 470 \uparrow + 125 \downarrow - 250.$$

Nothing whatever was to be seen of heterodromons relatively positive polarisation.

It is unnecessary to state, that all measures were taken to exclude direct actions of the shocks of the jar on the galvanometer, and that a clay model in the place of the preparation, showed at most the very faintest trace of negative polarisation.

I did not proceed further on this path, and I do not believe that any other result is to be attained here. But (§ 15) in a later experiment, which unfortunately only succeeded once, the heterodromous current actually produced relatively positive, absolutely negative polarisation.

7. The apparent irreciprocity of the conduction in the electrical organ increases with the current density.

In the first communication, I closed the examination of the nature of the homodromous, absolutely and relatively positive polarisation with the words, 'There is still one method of experiment at hand, which under certain conditions might lead to the attainment of the object, that is to observe whether with a longer closing time, the homodromous current maintains its preponderance. If this is the case, positive polarisation cannot be identified with the shock; for the latter, when the current goes for a long time through the organ, can only add itself to the battery current at the moment of closing. I have in fact seen this ascendancy with a closing time of 1″, 5″, or even 20″, but experiments of this kind will not be conclusive until the hypothesis of an irreciprocal resistance can be completely set aside.'

It is beyond question, that even with a much longer period of

closing the homodromous current is seen to preponderate. The result is obscured by two facts, first that the preparation conducts better when warmed, and secondly that the negative polarisation weakens the current; nevertheless by closing the currents for a minute by the hand, series are also obtained in which, in spite of all hindrances, the preponderance of the homodromous current declares itself plainly though feebly. Series of this nature will be communicated later (see below, § 12). Dr. Sachs' investigations on the organ of the Gymnotus also speak to the same effect[1].

Thus the question, whether the organ conducts irreciprocally in reality or only in appearance, lies directly across our path, and we must endeavour before all things to clear up this point.

The first thing that presents itself, is the very striking dependence of the phenomenon upon the current density, as is shown in the following experiments.

I sent the opening shocks of the inductorium, the primary coil of which was filled with wires, through the preparation from one skin surface to the other. The preparation rested in the usual way on the triangular plate between the clay shields of the conducting vessels. The galvanometer was in the same circuit. The shocks, produced by opening the mercury key, were by means of a Pohl's reverser, led through the preparation alternately in the homodromous and the heterodromous direction.

In the following table, *C D* denotes the distance of the secondary from the primary coil; the numbers are the deflections of the galvanometer. The great difference of the strengths of the shocks makes it necessary to put the bobbins at different distances from the mirror, and the deflections are therefore reduced to 5000 turns at a distance of 20 mm.

5. Torp. Fresh. $OC + 0{\cdot}0031$.

CD	=	0	↑	501	↓	215	↑	501	↓	215	↑	453	↓	215	↑	477	↓	191
„	=	10 cm.			↓	25	↑	28	↓	27	↑	28	↓	27	↑	27		
„	=	15 cm.					↑	7	↓	7	↑	7	↓	7				
„	=	0					↑	453	↓	227								

Taking the mean of the numbers of like signification, the ratio of the heterodromous to the homodromous deflections is

for *CD*	=	0	: :	212·3	:	477·0	: :	100	:	224·7
„ „	=	10 cm.	: :	26·33	:	27·66	: :	100	:	105·1
„ „	=	15 cm.	: :	7	:	7	: :	100	:	100·0.

Hence there can be no doubt, first, that the phenomenon becomes

[1] Untersuchungen, &c., p. 218; p. 224 of this volume.

observable by the means employed, when the current strength exceeds a certain limit, and secondly, that the irreciprocity increases with the current strength. By performing the experiment on preparations of different transverse section, one is convinced, thirdly, that the question here concerns not current strength, but, as was to be expected, current density. Fourthly, it follows from the above numbers, that within its sphere, irreciprocity increases more slowly than current density. If we take (see below, § 13) the difference between the homodromous and heterodromous current strength with the same transverse section, divided by the homodromous current strength, as a measure of the irreciprocity (a method of proceeding which will be justified later), then we find the irreciprocity

$$\text{at 10 cm. } CD = \frac{1{\cdot}33}{27{\cdot}66} = 0{\cdot}0481,$$

$$\text{at 0 cm. } CD = \frac{264{\cdot}7}{477{\cdot}0} = 0{\cdot}5549,$$

instead of $= 0{\cdot}8293$, as it would be if the irreciprocity were proportional to the current density. There can hardly be a doubt that the irreciprocity, referred to the current density, would approach asymptotically to a fixed limit.

8. The apparent irreciprocity of conduction in the electrical organ has its seat in every transverse lamella of the preparation, and increases with the length of the columnar tract which is traversed by the current.

I next convinced myself, that the difference in the strength of the currents becomes perceptible, not merely when they are led from the one polar surface of the preparation covered with skin to the other, but also between any points whatever of the lateral surfaces of the preparation, and the difference is the greater the further the points are separated from each other.

I again led the opening shocks of the inductorium, by opening the mercury key, through the preparation and galvanometer, but this time in accordance with the aim of the experiment, the preparation was not traversed by currents from skin surface to skin surface, but the clay points of the non-polarisable tubes, which took the place of the conducting vessels in the circuit containing the galvanometer and the secondary coil of the inductorium, were brought into contact with the lateral surface. The secondary coil

was pushed quite over the primary coil filled with wires. The distance of the bobbin (5000 turns) was 10 cm. from the mirror.

In Fig. 20 the curves denote the circuit, including the secondary and galvanometer coil. The preparation was taken from the fifth fish, killed the previous day; the organ current force amounted at first to + 0·0072.

When the clay points were in position (1), I obtained

↑ 42 ↓ 12 ↑ 42 ↓ 15 sc.;

in position (2),

↑ 38 ↓ 19 ↑ 38 ↑ 20 sc.;

finally, in position (3),

↑ 40 ↓ 22 ↑ 40 ↓ 22 sc.

According to this, there can be no doubt, that irreciprocal conduction, whatever may be its cause, has nothing to do with the skin; this was indeed already proved when I first observed it in the malapterurus preparations, where the skin constituted only an external closure.

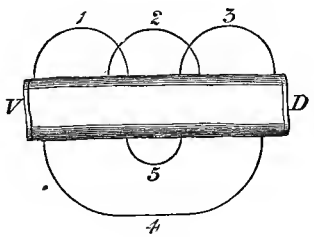


Fig. 20.

It might however still be supposed that its seat is superficial, that it depends on a resistance which develops itself only at the contacts of the clay points with the lateral surfaces of the preparation, after the manner of external secondary resistance. At first sight this is very improbable, considering that it increases evidently with current density, not with current strength; that it is observed even with such transient shocks as the opening shocks of an induction apparatus; that the interposal of the skin makes no change in its mode of appearance; and finally, that if one of the clay points, the positive or the negative, were the seat of a special resistance, this must be the case for homodromous currents just as much as for heterodromous.

But this conception would be quite impossible, if it were shown that the irreciprocity increases with the length of the columnar tract traversed by the currents. Now this is in point of fact the case.

A long tract of organ (4) gave

↑ 32 ↓ 12 ↑ 32 ↓ 13 sc.;

a short (5),

↑ 37 ↓ 29 ↑ 37 ↓ 29 sc.

If we take also the numbers of the tracts of medium length (1, 2, 3), then we find, as a mean of all numbers in the same category, the ratio of the homodromous to the heterodromous currents, in the long tract

100 : 39·1,

in the medium-length tracts,

100 : 45·8,

in the short tract,

100 : 78·4;

thus the longer the tract traversed, so much the greater is this ratio. The following numbers, which afford one of the most striking instances of irreciprocity, were obtained with the seventh torpedo on the second day, with a short distance (not indicated) of the galvanometer coil:—

Long tract.

↑ 217 ↓ 28 ↑ 160 ↓ 30.

Short tract.

↑ 176 ↓ 155 ↑ 176 ↓ 155.

Long tract.

↑ 165 ↓ 14 ↑ 165 ↓ 22.

The ratio of the current strengths with the long tract is

100 : 13·3,

with the short,

100 : 88·1.

One might object to this, that with a longer tract, the preparation forms a greater part of the total resistance of the circuit, and that this has misled us as regards the relation of greater irreciprocity to greater length. The slight difference between the homodromous current strength for long and short tracts shows that the resistance of the preparation, unquestionable as it may be in comparison with that of the clay points, forms a by no means large proportion of the total resistance of the circuit. However, it is desirable to establish safe from all doubt, a point so important as that of the increase of irreciprocity with the length of the tract traversed by the current.

The idea that the irreciprocity of conduction is influenced by the total resistance of the circuit, implies that it can be expressed by an additive term in the denominator of the fraction which represents the heterodromous current strength in Ohm's formula. Let us call this

term the *Irreciprocity-term.* According to our numbers, it seems to increase with the length of the tract traversed. If the objection raised against this is well founded, then it should be possible to represent the phenomena in a mathematical form, even when the term is assumed to be independent of the length of the tract traversed.

First of all, the question arises, in what way the dependence of the irreciprocity upon the current density is to be conceived of. This question cannot be answered with certainty. The best course seems to be to suppose that the irreciprocity increases with the homodromous current density, and indeed the small difference already pointed out between homodromous current strengths for longer and shorter tracts, allows us to assume the irreciprocity term to be proportional to this current strength without any considerable error, rather than to suppose that, in accordance with the previous paragraphs, it grows more slowly than it. We may proceed then further in the following way. Let us imagine, in place of the induction shock, that an equivalent portion of the short duration t is cut out of a constant current, and that E is the electromotive force of the cut-out portion. Next let

R denote the resistance of the circuit from clay point to clay point, containing the secondary coil of the inductorium and the galvanometer;

σ the specific resistance of the organ traversed longitudinally by the current, irrespective of irreciprocal resistance or with a homodromous current;

l the length of the long tract;

k that of the short tract of the organ;

q the cross section of the preparation[1];

I_l, I_k the homodromous;

I_{rl}, I_{rk} the heterodromous current strength for the longer and shorter tracts respectively;

$\sigma l/q$, $\sigma k/q$ the resistances of the long and short tracts respectively with homodromous current; finally,

$I_l c/q$, $I_k c/q$ the irreciprocity terms for the long and the short tract respectively, in which c is a constant.

[1] In the first communication (p. 454), in a similar consideration, we put the transverse section = 1. It would simplify the expressions and change nothing in the result if we did the same here, but the formulas are clearer if the transverse section appears in its proper place. Moreover, we neglect the circumstance that in our experiments, the current did not pass through the preparation from transverse section to transverse section, but from one clay point to the other applied to the preparation laterally.

Then we have

$$I_l = \frac{Et}{R + \frac{l\sigma}{q}}, \quad I_k = \frac{Et}{R + \frac{k\sigma}{q}},$$

$$I_{ll} = \frac{Et}{R + \frac{l\sigma}{q} + \frac{I_l c}{q}}, \quad I_{lk} = \frac{Et}{R + \frac{k\sigma}{q} + \frac{I_k c}{q}}. \qquad (a)$$

The irreciprocal resistance is made here dependent upon the dimensions of the tracts traversed by the current, only in so far as the homodromous current density, which is taken to be proportional to the irreciprocity term, depends upon those dimensions. Now according to our observations, irrespectively of the opposite signs of I and $I_{,}$, we must have

$$\frac{I_l}{I_{ll}} > \frac{I_k}{I_{lk}},$$

i. e. we must have

$$\frac{R + \frac{l\sigma}{q} + \frac{I_l c}{q}}{R + \frac{l\sigma}{q}} > \frac{R + \frac{k\sigma}{q} + \frac{I_k c}{q}}{R + \frac{k\sigma}{q}},$$

or

$$(qR + k\sigma) I_l > (qR + l\sigma) I_k. \qquad (b)$$

This is impossible, since for $R = 0$, or a mean value of R, the left side, factor for factor, is the smaller, and since, if all resistances are made to disappear in comparison with R, at the most, equality of both sides will be obtained. Consequently we do not succeed, when the irreciprocity term is assumed to be independent of the length of the tract traversed.

On the other hand, if in (a) we substitute

$$\text{for } (l\sigma + I_l c)/q \text{ and for } (k\sigma + I_k c)/q$$

$$\left(\sigma + \frac{I_l c}{q}\right) l/q \text{ and } \left(\sigma + \frac{I_k c}{q}\right) k/q;$$

i. e. if we treat the irreciprocal resistance as an increase of the specific resistance proportional to the current density when the current is a homodromous current, then we get instead of (b) the inequality

$$(qR + k\sigma) l I_l > (qR + l\sigma) k I_k. \qquad (c)$$

This indeed is still impossible supposing $R = 0$, for then it reduces itself to $I_l > I_k$. But if R has a great value, like that with which we are dealing, it approximates to the actually existing inequality $l > k$; and accordingly it may be considered proved that, other things being equal, the irreciprocity increases with the length of the tract of organ traversed.

9. The question, whether the appearance of irreciprocal conduction in the organ depends upon polarisation or conduction, cannot be answered by the introduction of additional resistance.

In the previous paragraph we set out with the hypothesis, that irreciprocal conduction may be expressed by an additive term in the denominator of Ohm's formula for the heterodromous current strength. This procedure, which has already proved available for our purpose, will be justified later; for the present, we must not forget that the question whether irreciprocal conduction depends upon unequal resistance in both directions, or upon polarisation, is still open. At first sight, the surest way to answer this question seems to be the mode of experiment mentioned already in the previous communication (p. 453), viz. to introduce into the primary circuit, a resistance in addition to that of the organ preparation so great, that the latter shall vanish. In this case, if the difference of the two currents should disappear, that of the polarisations persisting, the origin of the former difference would be shown to be the difference of resistance. In an experiment of this nature, in which I used a long narrow tube filled with physiological solution of rock-salt for the additional resistance, the difference of the current strengths in both directions did in fact disappear; but since, on account of lowered functional activity, the difference of the polarisation currents was also absent, no certain conclusion could be drawn from it. In the experiments of the previous paragraph, the apparent irreciprocity of the conduction was persistent, although the resistance of the preparation was but small in comparison with that of the rest of the circuit. It did not however disappear, and the polarisation was not observed, so that we cannot conclude from these observations that irreciprocity depends upon polarisation.

I have now carried out several experiments according to the method under consideration, with apparently good result. As liquid resistances are difficult to graduate and to estimate, I replaced the tube containing rock-salt solution by two plug rheostats of Siemens

and Halske, each of which has a resistance of 10,000 Siemens Units, and the coils of which are wound so as to be free from induction, as this might perhaps not be without importance here. By closing and opening a rubbing key which bridged the rheostat, its resistance was excluded or admitted at pleasure. I so conducted the experiment, that I sent through the preparation alternately a current of few Groves without the great additional resistance and one of many Groves with this resistance, and repeated it in homodromous and heterodromous direction alternately; the number of the Groves and the additional resistance being so arranged, that the current without resistance did not too much exceed that with resistance. Series such as the following were obtained, in which the notation requires no further explanation[1]. There were 50 turns for the galvanometer *P*, and 5000 turns for the galvanometer *S* at zero distance.

I.

2. Torp. Fresh. *L.* 19 mm. *OC* + 0·0128. 1′—*Per.*

CT 0″·0764.

X.—*S.*		−410	↑	+155		−210	↑	+20	‖	XXX.—	↑	+59		−32	↑	+29		−10	‖
P.	↓	114		143	↓	115		141	‖			75	↓	74		78	↓	77·5	‖

Without additional resistance. With resistance.

	−63	↑	+9		−51	↑	+8
↓	118		143	↓	118		149

Without resistance.

II.

New Preparation. *OC* + 0·0224. 1′—*Per.*

The same period of closing.

X.—*S.*	↑	+100		−92	↑	+141		−31	‖	XXX.—	↑	+80		−55	↑	+52		−37	‖
P.		187	↓	146		184	↓	148	‖			82	↓	80		82	↓	81·5	‖

Without resistance. With resistance.

X.—	↑	+57		−57	↑	—		−34
		184	↓	156		188	↓	157·5.

Without resistance.

III.

7. Torp. Second day. *OC* reversed, −0·0031. 1′—*Per.*

The same period of closing.

X.—*S.*	↑	+88		−35	↑	+70		−65	‖	XL.—	↑	+39		−63	↑	+15		−77	‖
P.		134	↓	189		119	↓	94	‖			92	↓	88		90·5	↓	89·5	‖

Without resistance. With resistance.

X.—	↑	+26		−42	↑	−Trace		−38
						+7		
		105	↓	95·5		104·5	↓	94·5

Without resistance.

These series fulfil the condition laid down, with sufficient exact-

[1] For explanation see Appendix to No. XII.

ness. In spite of the large amount of persistent polarisation, which is in favour of the homodromous and opposed to the heterodromous current, the additional resistance almost effaces the difference of the two currents. Accordingly it seems proved that the irreciprocal conduction rests upon resistance. Unfortunately, closer consideration showed that this time also, the mode of viewing the matter was not complete, and that it is impossible to decide between polarisation and resistance by this manner of experiment.

We will call as before :—

I the strength of the homodromous,

$I_,$ that of the heterodromous current ;

P the constant, which multiplied into the current density, measures the electromotive force of the homodromous absolutely and relatively positive polarisation for the unit length of the tract traversed ;

Π the corresponding constant for the relatively negative polarisation caused by both the currents ;

R the resistance of the circuit containing the battery and the galvanometer, exclusive of the resistance of the battery itself ;

n the small,

N the large number of Groves ;

G the electromotive force,

r the resistance of a single cell ;

W the additional resistance ;

σ the specific resistance of the organ when it is traversed longitudinally in both directions ;

l the length of the tract traversed, i. e. in this case of the preparation itself, provided that the resistance of the skin is to be included in R ; finally,

q its transverse section.

Then, with the small number of Groves and without additional resistance, we have

$$I = \frac{nG - l.\frac{I}{q}(\Pi - P)}{nr + R + \frac{l\sigma}{q}}. \qquad (d)$$

$$I_, = \frac{nG - l.\frac{I_,}{q}\Pi}{nr + R + \frac{l\sigma}{q}}. \qquad (e)$$

The two polarisations are here both taken to be proportional to the current density as in the first communication (pp. 455). It is self-evident that they are also proportional to the length of the preparation.

The question whether we can decide between the two possibilities in this way, is answered in the negative by the very statement of the above formulas. More than fifty years ago, when treating of the similar question as to the existence of a transition resistance besides the polarisation of the electrodes, G. S. Ohm directed attention to the fact that in such expressions as (*d*) and (*e*) the way in which polarisation and resistances severally enter is only apparent, that polarisation therefore stands in the same relation to an additional resistance as the constant resistances do, and that it cannot be distinguished from these by the introduction of an additional resistance.

We find in fact

$$I = \frac{nG}{nr + R + \frac{l}{q}(\sigma + \Pi - P)}, \quad I_l = \frac{nG}{nr + R + \frac{l}{q}(\sigma + \Pi)},$$

and if for sake of brevity we put

$$nr + R + \frac{l}{q}(\sigma + \Pi) = \Lambda_n$$

$$I = \frac{nG}{\Lambda_n - \frac{lP}{q}}, \quad I_l = \frac{nG}{\Lambda_n},$$

$$I - I_l = \frac{nGlP}{\Lambda_n(q\Lambda_n - lP)}. \qquad (f)$$

This expression is finite and positive, so long as $q\Lambda_n > lP$; $q\Lambda_n = lP$ would make I infinite, and $q\Lambda_n < lP$ would give the upper hand to the heterodromous current. By introducing the additional resistance and exchanging n for N, (f) becomes

$$I - I_l = \frac{NGlP}{(\Lambda_N + W)(q(\Lambda_N + W) - lP)}.$$

When W is great, this expression approaches to the value

$$I - I_l = \frac{NGlP}{qW^2},$$

i. e. to zero, and hence these formulas, in which the irreciprocal resistance is left out and regard had only to polarisation, sufficiently represent the facts of the case, as now presented to us.

The result comes under the same form, if we put the positive polarisation P independent of I instead of proportional to it; this corresponds better with the hypothesis, according to which it is only the after-effect of a shock, for in this case we have simply

$$I - I_1 = \frac{lP}{\Lambda_n}$$

without additional resistance, and

$$I - I_1 = \frac{lI}{\Lambda_N + W}$$

with such resistance and many Groves. The first expression is positive, the second approximates to zero as W increases.

Consequently, according to the observations up to the present time, in spite of all appearance, it is not necessary to assume irreciprocal resistance in order to explain how the fact stands. It is so improbable, that the absolutely and relatively positive polarisation by the homodromous current could effect an increase of this current in comparison with the heterodromous in the ratio of 100 : 13·3 (see above, p. 507), that the decision sought for cannot be arrived at in this way, and we must seek for it in another experimental field.

10. Measurements of the resistance of the electrical organ of the torpedo.

Quite apart from all other questions attaching to the subject, it was naturally of great interest to ascertain something about the conduction of the organ in comparison with the other tissues. The mode of procedure was given by the experiments which I performed in 1871 in connexion with the resistance of the muscle of the frog, that of physiological rock-salt solution and of clay prepared with it[1], in which I made use of the contrivance employed first by Ranke, viz. to enclose the tissue, liquids, etc. in glass tubes of equal dimensions, in order to give them a prismatic form, equal length

[1] Gesammelte Abhandlungen, vol. ii. p. 373 f.

and equal transverse section[1]. As regards the details of the method, I refer to the description given at that time. But in order to make it more readily understood, and inasmuch as the apparatus in all its simplicity has proved well suited to our object, I add a diagram of it in Fig. 21 in a somewhat more perfect form. The new apparatus differs in some points from my original model. It is unessential that the funnels, which, filled with physiological clay, connect the base of the tube containing the tissue etc. with the leading-in pads, are made of vulcanite instead of gutta-percha, and are supported by brass pillars well lackered; it is of greater importance that the diameter of their apertures very little exceeds the thickness of the pads; hence the side of each cone is still only 12·5 mm. long. Their resistance is thereby considerably diminished, and this is advantageous, in so far as it is desirable that the resistance of the rest of the circuit should be as small as possible in

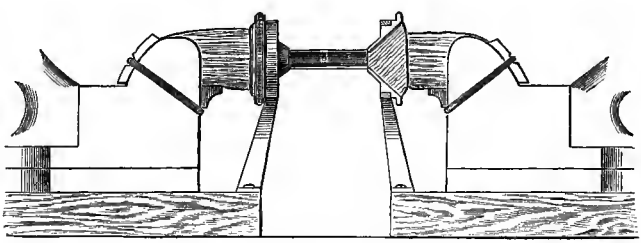


Fig. 21.

comparison with that of the conductor of which the resistance is to be determined. In the figure, it is easy to recognise the funnel filled with clay, drawn on the left in elevation and on the right in section, between the leading-in vessels and the resistance tube fixed between the funnels.

The tubes previously used, 25 mm. in length, with an internal diameter of 4·6 mm. are exactly suited for the M. gracilis of a frog, 22 cm. in length from the tip of the nose to the longest toe, a medium size readily found in this country[2]. I still had the very same tubes in my possession; it was found that they had also the length and breadth suitable for organ preparations. In order to introduce these into the tubes so as to fill them completely, I drew

[1] Joh. Ranke. Tetanus. Eine physiologische Studie. Leipzig, 1865, p. 44.

[2] Ueber secundär-elektromotorische Erscheinungen. Sitzungsberichte, 1883, vol. i. p. 355.

a thread through the dorsal or ventral skin of the preparation and pulled the preparation into the tube by the thread. Any ends which might happen to project were cut off. I often helped to get it into the tube by sucking. In doing this, it happened that I sucked the preparation quite through the tube into my mouth. To my surprise, I found that the organ was quite insipid, without a trace of the salt taste I had expected in accordance with Boll's statement on the *Liquor cerebrospinalis* of the Torpedo[1].

According to Boll's estimate, the tissues of the Torpedo contain a salt solution of 2.5 per cent., so that only a solution of sodium chloride of this strength would be 'physiological' to them. According to Léon Fredericq the blood of the *Octopus vulgaris* and *Astacus marinus* contains about four times more salts than that of mammals. Hence I suspected that the tissues of marine animals, especially of sea fishes, would be richer in salt than those of fresh-water animals, and that they would also conduct better accordingly. They would thus be more strongly affected by the current curves with which a Torpedo shock fills the sea around it, than if they had only the same proportion of salt as fresh-water animals, for these curves are attenuated in a badly conducting body plunged in the sea[2]. That it would be of service to the Torpedo if its own organ conducted better, seemed quite obvious. But the state of the case is otherwise.

First of all, it was found that the tissues of sea fish are not perceptibly salter than those of fresh-water fish. It could not be concluded with certainty from Atwater's and König's tables that sea fish are richer in salt, and Weyl found that the organ of the Torpedo yielded only a little more ash than the muscle flesh of river fish (p. 437)[3]. But Fredericq had observed what had escaped me, that the characteristic which he had recognized at the date of my first communication in the invertebrate marine animals, is absent in sea fishes—*Trachinus spec.*, *Solea vulgaris*, *G. Aeglefinus* (a shark)—and he was thus led to regard the circumstance that the amount of salt contained in the fish is so independent of the medium in which they live, as an indication of their higher organi-

[1] Monatsberichte der Akademie, 1875, p. 710; Archiv für Anatomie, Physiologie, 1875, p. 463, note.

[2] Untersuchungen, &c., pp. 133, 415.

[3] Comp. also Almén, in Maly's Jahresbericht über die Fortschritte der Thier-Chemie, vol. vii. 1877, p. 308.

sation as compared with that of the invertebrates[1]. Boll, who judged merely by the taste of the *Liquor cerebrospinalis*, was perhaps deceived by the amount of urea discovered by Frerichs and Städler in the juices of the tissues of the skate[2].

However that may be, the organ of the torpedo, far from conducting particularly well, does not conduct as well as frog's muscle in the longitudinal direction. In the following statements, i according to the index attached to it, denotes deflections in scale divisions of the aperiodic mirror (with 5000 turns at 100 mm. distance) by the opening shock of the inductorium, when the primary coil was filled with rods and the secondary coil pushed up. The resistances indicated were placed between the clay cones. i_o denotes that resistance between the clay cones was nil; i_{lg}, i_{lw}, i_{sw} are the deflections with the tube full of $\frac{3}{4}$ per cent. rock-salt solution, full of tap-water and full of sea-water respectively; i_m is the deflection with the tube full of frog muscle; finally, i_{ho} and i_{he} are the deflections with the organ in the tube traversed by the homodromous and heterodromous current respectively, w_o, w_{lw}, w_{sw} w_m, w_{ho}, and w_{he} are the corresponding specific resistances referred to the $\frac{3}{4}$ per cent. rock-salt solution w_{lg} as unity.

A first series of experiments were performed last summer on the second Torpedo, on the third day, still using the original apparatus which had served for the experiments of 1871 already described. The three organ preparations, the resistance of which was determined with homodromous and heterodromous direction of current, showed the organ current in the right direction and of considerable strength. The result of five determinations in both directions, differing but little from each other, gave a mean of

$$i_o = 66{\cdot}7,\ i_{lg} = 49{\cdot}2 \text{ sc.}$$

In this condition, without tube, or with the tube full of physiological rock-salt solution, the apparatus showed no perceptible irreciprocity of conduction.

The organ preparations gave respectively:

I. $i_{ho} = 36{\cdot}0, \ldots i_{he} = 31{\cdot}0.$
II. $i_{ho} = 31{\cdot}2, \ldots i_{he} = 23{\cdot}0.$
III. $i_{ho} = 29{\cdot}0, \ldots i_{he} = 8{\cdot}8.$

[1] Bulletins de l'Académie royale des Sciences . . . de Belgique, 3me Série, vol. iv. No. 8, Août, 1882, p. 209.

[2] Erdmann's und Werther's Journal für praktische Chemie, 1858, vol. lxxiii. p. 48.

Thence we find, putting $w_{lg} = 1$, according to the formula

$$w_{ho} : w_{he} : w_{lg} :: \frac{1}{i_{ho}} - \frac{1}{i_o} :: \frac{1}{i_{he}} - \frac{1}{i_o} : \frac{1}{i_{lg}} - \frac{1}{i_o},$$

I. $w_{ho} = 2{\cdot}397, \ldots w_{he} = 3{\cdot}238.$
II. $w_{ho} = 3{\cdot}199, \ldots w_{he} = 5{\cdot}342.$
III. $w_{ho} = 3{\cdot}655, \ldots w_{he} = 18{\cdot}50.$

This very surprising result induced me to determine again the resistance of frog muscle in comparison with the physiological rock-salt solution, and on the same occasion, that of the artificial sea-water of the Berlin aquarium, which had a specific gravity of 1·0250 at 22·75° C., and was thus apparently somewhat higher than on the occasion of Prof. Christiani's determination of the conducting power of sea-water[1]. This time

$$i_o = 60{\cdot}9 \text{ sc.}, \; i_{lg} = 48{\cdot}0 \text{ sc.}, \; i_m = 40{\cdot}0, \; i_{sw} = 56{\cdot}5 \text{ sc.},$$

whence resulted

$$w_m = 1{\cdot}9383, \; w_{sw} = 0{\cdot}3202.$$

I had previously (1871) found $w_m = 1{\cdot}9045$; the difference amounts to $\frac{1}{57}$; a closer agreement is scarcely to be expected in determinations of the kind.

I undertook a second similar series of experiments on the third Torpedo, on the second day of experimenting. I omit the observed deflections, and give at once the values calculated from them, that is to the specific resistances of three other preparations, through which currents were led homodromously and heterodromously. These exhibited powerful organ currents. Their specific resistances are stated below in terms of that of physiological salt solution :—

IV. $w_{ho} = 3{\cdot}5983, \ldots w_{he} = 13{\cdot}5517.$
V. $w_{ho} = 3{\cdot}3741, \ldots w_{he} = 6{\cdot}2752.$
VI. $w_{ho} = 3{\cdot}7781, \ldots w_{he} = 6{\cdot}2752.$

On the same occasion, I determined the resistance of the tap-water w_{lw} at 37·955. It was interesting to consider how these determinations of sea- and tap-water would agree with those obtained by Prof. Christiani by another method, and which are

[1] Untersuchungen, &c., p. 413.

communicated in the book on the gymnotus loc. cit. In Prof. Christiani's experiments the tap-water conducted 126·57 times worse than the sea-water of the Aquarium. Our numbers give

$$0{\cdot}3202 : 37{\cdot}955 = 1 : 118{\cdot}52.$$

A closer agreement is scarcely attainable in such circumstances.

It is apparent that even in the homodromous direction, in which the organ conducts best, it conducts scarcely half as well as frog muscle parallel to the fibre, and 7·5 to 12 times worse than the sea-water of the Aquarium. The ratio would be still more unfavourable with sea-water from the Mediterranean, which conducts nearly 150 times better than tap-water. But in the heterodromous direction, the organ conducts even 20 to 58 times worse than sea-water.

Our method does not allow of our obtaining corresponding numerical determinations for the transverse conduction of the organ. That the electrical organ does conduct quite reciprocally in a transverse direction, I showed a long time ago in the case of the Malapterurus, where it is easy to cut strips of the organ vertically to the direction of shock. I now endeavoured to ascertain, for the organ of the Torpedo at least, how transverse conduction compares generally with homodromous and heterodromous conduction. I cut from the organ square slices as uniformly thick as possible, of which one edge was formed of dorsal skin, the opposite one of ventral skin, and the two lateral edges were formed of lateral surfaces of the columns, and sent induction shocks through them, sometimes from belly to back, sometimes from back to belly, sometimes in transverse direction from one lateral edge to the other. In the homodromous direction, the deflections were, for example, 80·7, in the heterodromous 22·5, in transverse direction each way 99. The suspicion might arise that the semblance of better conduction in the transverse direction, is the result of the skin on the dorsal and ventral edge of the slice increasing the resistance, when it is traversed longitudinally. But when I covered the lateral edges with pieces of skin and sent the current through these, the deflection was still 95 sc.; after removing the artificial covering of skin the deflection was the same, the homodromous on the other hand being now only 75, the heterodromous 18. It thus seems as if the organ conducts in transverse direction, even better than in homodromous. However, I consider this result as not yet certain, on account of the defectiveness of the mode of experiment.

11. Dependence of the irreciprocal resistance and of the resistance of the organ in general upon its vital condition.

The small conducting power of the organ and its irreciprocity are closely connected with its vitality. If the tube was filled with columns which projected at both ends, and plunged in boiling water for several minutes, in consequence of which the organ acquired an acid reaction, it remained filled with organ in spite of the shrivelling of the columns by the boiling. I have already stated that boiled organ conducts better than living organ (p. 458). I am now able to add, first that its resistance becomes exactly the same in both directions, secondly that after cooling it sinks below the minimum resistance in the homodromous direction, and is even smaller than that of physiological salt-solution. Compared to this as unity, I found it to be only = 0·9294.

The course of events is similar when the organ dies a natural death, only it is evident that a longer period is required. Here, also, homodromous and heterodromous resistance approximate to equality, and homodromous resistance diminishes. Naturally the dead organ, especially in a more advanced stage of decomposition, is ill-fitted for preparations which have to be drawn into the resistance-tube. Preparations taken from such an organ, as I remarked long since (p. 439), have a tendency to assume an hour-glass form between the more compact dorsal and ventral skin which covers their polar surfaces. However, it is possible with some patience to obtain determinations like the following.

The organ of the seventh Torpedo, kept at a low temperature, had an indistinctly acid reaction fifty-five hours after death. It had already a smell of ammonia, and thus the acid was probably neutralized by the ammonium carbonate arising from the decomposition of urea in the tissues, as might be proved by the reaction being acid only here and there in the muscles. The preparations acted feebly in homodromous direction; however, this could hardly be the organ current, but rather an electromotive action produced by an acid and an alkaline liquid accidentally coming in contact with each other in the interior of the organ. A first preparation gave

$$w_{ho} = 2{\cdot}968, \ldots w_{he} = 3{\cdot}231.$$

Thus the irreciprocity amounted to only eight per cent. of the homodromous current strength. But in another preparation, it was

directly afterwards entirely absent; the resistance in either direction was as follows:—

$$w_{ho} = w_{he} = 2{\cdot}317.$$

On the following day, seventy-six hours after death, with evident decomposition, no difference of homodromous and heterodromous conduction could be any longer perceived, and I found in two preparations

$$w_{ho} = w_{he} = 1{\cdot}0826 = 0{\cdot}8553.$$

Thus in the latter case, the resistance was less than that of physiological salt-solution, and even of the boiled preparation.

It may be asked, whence may the considerable variations in the heterodromous resistance of the organ arise? It is probable that the largest numbers found for it are the most accurate, and the smallness of the other values depends upon a double cause. First, it is undoubtedly injurious to the functional activity of the columns, that they are squeezed by drawing them into the resistance-tube. Secondly, it is certain that, in doing this, some if not all of the plates must lie more or less obliquely in the tube, and hence the heterodromous resistance, which is connected with the perpendicular direction of the current in regard to the plates, is necessarily lowered.

It would have been desirable to determine the conductivity of other tissues of the Torpedo also, especially of its muscles. But, in the first place, I have not hitherto found in the Torpedo any muscle which is available in any measure as a regular muscle, comparable to certain thigh muscles of the frog, the sartorius of the dog, and others. Secondly, at the commencement of the experiments, I had to turn my attention to more important questions in the case of each fish, and in the few cases, when I intended to experiment upon the muscles, I found them already more or less functionally inactive, and indeed with an acid reaction to some extent. This is likewise the reason, why I am still unable to say anything about the electromotive force of the muscles of the Torpedo.

12. The conduction of the electrical organ when investigated by means of constant currents.

As regards the electrical organ, it seems impossible to doubt any longer, according to the above, that it conducts irreciprocally. If there is no such conduction, we are compelled to attribute to the

absolutely and relatively, positive, homodromous polarisation an electromotive force which may amount to that of twenty Groves (pp. 453, 454). If such a force were the cause of the superiority of the homodromous current, how could it be explained that even in homodromous direction, the preparation conducts worse than physiological salt-solution, or even than frog's muscle? It cannot be maintained that the smallness of the current strength as compared with the tremendous homodromous force is dependent on bad conduction, for even the heterodromous conductivity is not bad enough for that. Besides this, if the superiority of the homodromous current depended upon polarisation, it would be impossible to conceive how on the death of the organ, or on boiling it, the conductivity for both currents becomes the same and then absolutely increases, so that it even exceeds that of physiological salt-solution. The enfeeblement of the current cannot therefore be a consequence of the falling off of an electromotive force in the same direction with it.

It seems, as has already been said, impossible to escape the weight of these reasons, and the existence of irreciprocal conduction in the electrical organ is to be regarded as an established fact from henceforward. However, a considerable change in our conception of this remarkable property of the organ is to be looked forward to.

I now recollected that I had carried out these experiments, otherwise to all appearance conclusive, with induction shocks only. It occurred to me that in the series of observations mentioned above, p. 503, in which the current of a Grove's battery was closed for a longer period through the preparations, the superiority of the homodromous current continued indeed perceptible, but by no means so considerable as in the experiments with induction shocks, or with battery currents of short duration. I now began to suspect that the irreciprocity of conduction must depend, not only on the density but also on the duration of the current, and this was found to be the case.

Instead of the secondary coil as in the previous experiments, a Grove's battery was placed directly in the circuit of the galvanometer, on the mirror of which, only 45 turns acted from a suitable distance. The battery current was closed through the mercury key by hand for any desired period as timed by the clock. If for a short time only the contrivance mentioned above was employed (p. 481, note). When required, it was exchanged for the secondary coil of the inductorium, which was pushed quite up to the primary

coil filled with rods. The preparations lay upon the triangular glass-plate, with ventral and dorsal skin between the clay shields of the leading-in vessels. In the following series of experiments, 'long closing' signifies that the battery was kept closed as long as was possible, without too much interference by heating, polarisation, etc. All the deflections are reduced to the magnitude which they would have had with the 45 turns at zero distance.

First Series.

6. Torp. Fresh.

Grove's Battery.

Long closing.

I.—↑ 223 ↓ 223 ↑ 223.

There is no appearance of any irreciprocity of conduction.

Long closing.

V.—↓ 1128 ↑ 1159 ↓ 1140 ↑ 1177.

Certainly some irreciprocity, even though feeble.

Long closing.

XX.—↑ 4439 ↓ 4658 ↑ 5098 ↓ 4927.
−219 −440 +171.

A disturbance due to heating of the preparation and of the clay shields is observable, so that irreciprocity makes its appearance evident only in the series of differences.

Induction Shocks.

↑ 15 ↓ 3; 3 ↑ 15; 15.

This shows, that when the preparation is treated with shocks of short duration only, the irreciprocity of conduction is manifested in full extent.

Grove's Battery.

Long closing.

XX.—↑ 4756 ↓ 4781 ↑ 4903 ↓ 4890.
−25 −122 +13.

Again, irreciprocity shows itself in the series of differences only.

C. T. 0″·0310.

XX.—↓ 86 ↑ 95 ↓ 84 ↑ 95.

With short closing, it appears distinctly at once, although less decidedly than with opening shocks.

Long closing.

XX.—↓ 3927 ↑ 4318 ↓ 4207 ↑ 4634.

In spite of collateral effects, it manifests itself this time with long closing, the series of differences not being stated.

The preparation was not displaced throughout the whole series of experiments.

SECOND SERIES.

6. Torp. Second Day.

Grove's Battery.

C. T. 0″·0310[1].	Long closing.	*C. T.* 0″·0310.
I.— ↑ 2·55 ↓ 1·45 ↑ 2·61 ↓ 1·34	‖ ↑ 30 ↓ 29 ↑ 30 ↓ 30·5	‖ ↑ 2·66 ↓ 1·48 ↑ 2·58 ↑ 1·85.

Thus even with only one Grove, under favourable circumstances, irreciprocity of conduction shows itself for short closing, whilst for long closing it is only very feebly pronounced, so that in the corresponding experiment of the first series, it was not perceived at all.

C. T. 0″·0310.	Long closing.
V.— ↑ 20 ↓ 17 ↑ 19·5 ↓ 15	‖ ↑ 878 ↓ 866 ↑ 902 ↓ 866.

C. T. 0″·0310.	Long closing.
XX.— ↑ 115 ↓ 95 ↑ 120 ↓ 95	‖ ↑ 5073 ↓ 5415 ↑ 7073 −342 −1658.

The heating of the preparation prevented further observation; the irreciprocal conduction nevertheless makes itself noticeable in the series of differences.

The last experiment of the appendix of the first communication (25) is allied to these experiments, as being of similar interpretation. There, the current strength in the circuit of a battery of twenty cells closed through a preparation, and at the same time in a side circuit, by which the preparation was bridged, was observed. For short closing, the irreciprocity was very great; if the closing lasted one second, it was already disproportionately feebler.

13. Of the law and the nature of irreciprocal conduction in the electrical organ.

In accordance with the preceding, there can be no doubt, that irreciprocity of conduction is disproportionately greater for short closing of a battery and for opening shocks of an inductorium, than

[1] Here, instead of 45 turns at zero distance, 5000 turns were used at a distance of 30 mm. The deflections are diminished in the ratio 45/5000, and are reduced to the distance zero of the coil (comp. 454).

for longer closing, and that the numerical determinations of § 10, in as far as they refer to heterodromous conduction in the organ, are only correct for opening induction shocks. The two-fold dependence of irreciprocal conduction upon density and duration of current may now be represented graphically in the following way.

In Fig 22 the Δ-axis of the current densities runs from the zero point forwards and to the left, and the *T*-axis of the times of closing, forwards and to the right. The abscissae independent of

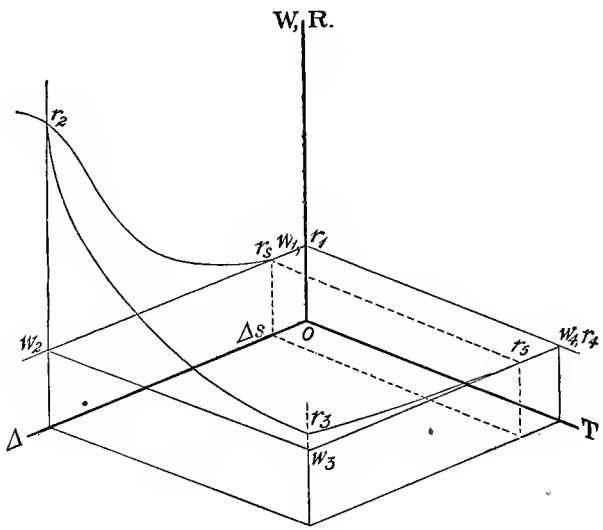


Fig. 22.

each other on both axes are measured arbitrarily. The homodromous resistances *W* and the heterodromous resistances *R* are expressed as ordinates on the *T*-Δ-plane. The homodromous resistance is independent of current density and duration, and thus the ordinates representing it, have throughout the same arbitrarily chosen height Ow_1, and their tops all lie in the plane $w_{1,2,3,4}$ parallel to the *T*-Δ-plane. The heterodromous resistance is not perceptibly different from the homodromous resistance, below the current density Δ_s; the irreciprocity is here apparently zero. Whether it is so in reality, is not yet decided, for I have unfor-

tunately postponed the repetition of the experiments with feeble opening shocks with a galvanometer of greater sensitiveness, and it is possible that a difference, too small to be detected by the galvanometer of the sensitiveness employed above (p. 517), might thus be proved to exist. However that may be, it may be assumed for the present, that to the right of and above the line Δ_s (the threshold line) with the means of observation actually used, the tops of the ordinates, representing the heterodromous resistances, seem to lie in the plane $r_{1,\ ,5,4}$ parallel to the T-Δ-plane. But to the left of this line, the heterodromous resistance becomes so much the greater, as the density is greater and the time of closing is less. Thus with increasing density and decreasing closing time, the tops of the ordinates r rise above the plane $w_{1,2,3,4}$, so that they lie in the surface of complex curvature $r_{1,2,3,4}$. It is to be assumed that the heterodromous resistance, with increasing current density, approaches a limit (see above, p. 505); this is expressed by the course of the curve of heterodromous resistance for minimal duration of closure, which as it nears r_2 becomes concave towards the axis. With increasing duration of closing, it approaches an inferior limit, as is expressed by the curve $r_{2,3}$, which unites itself asymptotically with $w_{2,3}$; that is with a line parallel to the time axis; there will however be somewhat to remark upon this later on.

This gives upon the whole the main features of the law of the phenomenon. The mode of formulating irreciprocity (pp. 504, 505) seems now to be sufficiently justified. It is at present impossible to form a satisfactory conception as to the cause of the phenomenon. At first the idea may occur, that it is somewhat similar to the internal secondary resistance, which I have described in the case of a porous moist conductor, in which the internal resistance increases with the current density[1]. The analogy between the two phenomena is however scarcely a true one. The internal secondary resistance has this indeed in common with heterodromous resistance, that boiling temperature destroys it. But disregarding the fact that hitherto it has been observed in living tissue of plants only, it is independent of the direction of the current, it demands longer time of closing for its development, and, when once developed, longer time for its disappearance, whilst, on the contrary, heterodromous resistance is present to its greatest extent at the

[1] Gesammelte Abhandlungen, vol. i. pp. 90 f., 116 f.

first moment, falls with longer duration of the current, and shows itself again in full force when the current is again closed for a short time.

It seems rather, that we must suppose that the heterodromous current, as soon as its density surpasses a certain value, the threshold value in the preparation, meets with a special resistance, and that a certain time is required to overcome it. This would explain why irreciprocity of conduction is more strongly developed with current impulses of short duration, while comparatively little is left if the current is of longer duration.

The small amount of irreciprocity when the flow is continuous, may perhaps not be dependent on the same cause as the extreme irreciprocity with currents of minimal duration. For a remark made in the first communication (p. 456) ought not to be forgotten here. Inasmuch as there is no doubt of the existence of homodromous positive polarisation, it must be regarded as a concomitant cause of apparently irreciprocal conduction, even though this is actually traced to an unequal resistance in the two directions. But when the time of closing is long, the irreciprocity becomes so small, that we have no longer the same ground for holding it improbable, as at first sight seemed necessary, that it is solely due to polarisation, that ground being the enormous electromotive force, amounting to many Groves, which that explanation obliged us to ascribe to polarisation. When the time of closing is long, the difference of current strengths, so far as the disturbances due to heating etc. allow of its being estimated, amounts to a few percentages, so that with twenty Groves in the circuit, a polarisation force of less than one Grove would suffice to explain the irreciprocity. If this view of the matter should be confirmed, then irreciprocity of conduction might be entirely connected with short duration of current. The curve $r_{2,3}$ in Fig. 22 would then merge into the straight line $w_{2,\ 3}$, instead of a line above it and parallel to it.

It is not necessary to say that the mechanism of irreciprocal conduction in the long direction of the columns remains in complete obscurity. We must not enter here, upon what is already known as to irreciprocal conduction in galvanic and induction circuits, all of which is to be found collected in Prof. Christiani's book[1]. We may state as probable that it is not nerves, vessels, or

[1] Beiträge zur Electricitätslehre. Über irreciproke Leitung electrischer Ströme, &c., Berlin, 1876.

connective tissue to which this property belongs, but the electrical plates themselves. It cannot depend upon Boll's striations, because besides the difficulty of understanding how this could be the case, the malapterurus plates are striated on both surfaces[1]. Since death and boiling heat put an end to irreciprocity, it seems as if it must be connected in some way with the function of the plates. In the first communication (p. 453) I endeavoured to explain the worse heterodromous conduction, by supposing that the heterodromous current is almost or quite incapable of rotating the hypothetical electromotive molecules in such a way, that its positive pole may face the negative surface, which in the torpedo is the ventral surface of the organ. At first sight, it seems in accordance with this supposition, that the resistances become the same in both directions in the dead organ, in which the hypothetical molecules have ceased to act. But the difficulty arises that they decrease at the same time, so that they become less than the smaller of them was during life. If the electromotive molecules, by virtue of the different electro-chemical nature of their poles, were considered in electrolytic conduction as molecules made up of electro-positive and electro-negative substances according to Grotthuss' theory, then we should expect, on the contrary, that the dead organ would conduct worse in both directions, than the living organ in the heterodromous direction. It is, however, no way out of the difficulty to say that the organ by itself, without the aid afforded by the electromotive molecules, conducts as badly as it does when traversed by heterodromous currents during life, and that owing to alteration in the dead body, formation of acid, etc., it conducts better than when traversed by homodromous currents during life.

14. Teleology of irreciprocal conduction in the electrical organ.

We have been frequently reminded in the course of these studies, of the difficulty which the older physicists and physiologists, from Volta and Nicholson to Faraday and Valentin, found in explaining the actions of electrical fish, without insulating septa; these they supposed placed laterally about the organs, or that they came into existence at the moment of the shock. The first fruit of my labours in this department was the removal of this error, more than

[1] Untersuchungen, &c., pp. 291, 391, 392.

forty years ago. For histological reasons, I doubted the existence, and even the possibility, of such investments, and I proved, at first only theoretically, but later by experiments with schemata, that multiplication of the electromotive elementary action in the surrounding conducting medium does take place, although a battery so formed must be considered as imperfect[1].

We now learn, that in the electrical organ there exists a sort of conduction of which the counterpart is hitherto nowhere known. Every fresh characteristic of this wonderful structure must excite attention, inasmuch as the hope of attaining a glimpse of its electrical mechanism is bound up with it. But irreciprocal conduction has a very special interest, inasmuch as it appears to perform for the organ, a function similar to that of insulating coverings, and it would even seem to accomplish this much more completely. The very fact that we succeeded so little in acquiring an understanding of the essence of this property, tends to enhance the gratification which we feel in the discovery, that it plays a not unimportant part in the economy of the shock of the electrical fish. The following consideration will make this intelligible.

Let us imagine first, a single column of the Torpedo's organ, surrounded by an unlimited conducting mass. For the present we will disregard all distinctions of ordinary and irreciprocal resistance and of polarisation, and picture to ourselves the column as constantly active. It is not difficult to give a general idea of the system of current curves, with which the column fills space. In the first place, it is evident that this system is distributed symmetrically about the axis of the column. Further, it is symmetrical also in regard to the plane which cuts it in half, and which is perpendicular to the axis. To make the subject more intelligible, we will call this plane the transverse median plane, the positive dorsal end of the column will be called the superior, and the negative ventral end the inferior.

Current curves issue from the positive dorsal surface of the column, and also from points of the lateral surface above the median transverse plane. All the curves cut the median transverse plane *o o* perpendicularly; this plane is in fact the isoelectrical surface of which the tension is o. The curves issuing from the

[1] Vorläufiger Abriss einer Untersuchung über den sogenannten Froschstrom und über die elektromotorischen Fische. Poggendorff's Annalen, 1843, vol. lviii. p. 25 f. Gesammelte Abhandlungen, vol. ii. p. 678 f. Untersuchungen, &c., pp. 259, 284, 300.

lateral surface, re-enter it below the transverse median plane, and the curves starting from points of the dorsal surface, enter at corresponding points of the ventral surface. The prolongation of the axis is a current curve which loses itself in infinity. In the interior of the column, currents flow from the belly to the back,

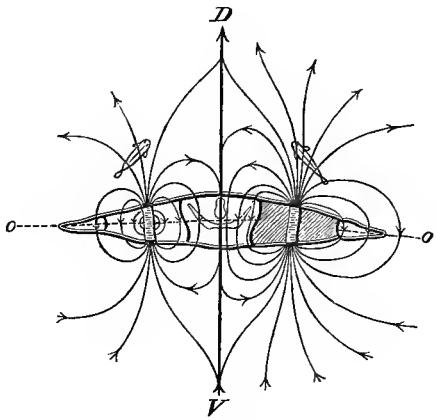


Fig. 23.

those near the axis being nearly parallel to it, those nearer the lateral surfaces, diverging from each other, so that the curves cut the lateral surfaces. To the left of the figure, distorted for a reason to be mentioned immediately, the diagram represents the intersection of the outer system of curves with the transverse plane of the fish round a single column supposed to be active.

If we imagine in the unlimited conducting mass, a second exactly similar column by the side of the first column, its axis parallel to that of the first, its dorsal and ventral surface in the same plane, so that the transverse median planes belonging to both columns would coincide, then the second column fills space with a system of curves precisely similar to the first. The current threads belonging to both the systems, compound themselves in any element of surface whatever of space, according to the parallelopiped of forces, in conformity with the principle of superposition of currents[1]. The case is precisely similar as regards a third, a fourth, or an nth column. If the distances of the columns from each other and their mass

[1] Comp. Helmholtz in Poggendorff's Annalen, 1853, vol. lxxxix. p. 212 f.

vanish, as compared with the distance of the element of surface under consideration, then the density of the current in the element is doubled by the addition of the second column, trebled by that of the third, and multiplied n times by the addition of the nth column. As the distance of the element of surface diminishes, the density of the current increases in it more slowly with the addition of new columns and in a very complicated manner, but it constantly increases with the number of columns. As each column represents for all other columns, a portion of external space, each one will be met by a portion of the current threads of the others, for the most part heterodromously, and the components of the external currents are deducted in the interior of the column from those of its own current. This is what I call the principle of imperfect pile formation, and thus it is comprehensible, how without insulating coverings, a multiplication of elementary effect is possible in electrical organs.

Further consideration is simplified by the remark, that since the Torpedo possesses two organs symmetrically placed, it is sufficient to fix the attention on one column symmetrically placed in each organ. The sagittal plane *VD* of the fish, when extended to infinity, is a surface of flow for the process of flow due to both of these columns. Consequently we can think of it as insulated, without changing anything in the process, or we may also halve the infinite conducting space in this plane, and we require to investigate only what takes place in one half of it.

It is clear from the above, that all other columns of an organ are traversed heterodromously by the current threads of the one column under consideration, as is shown in Fig. 23 to the left of the sagittal plane. If we fix our attention upon a portion of external space, e.g. the little fish seen in the figure, then the rest of the current threads form a collateral channel of closure for the current threads which meet the little fish. The worse this conducts, so much the stronger is the shock which the fish receives. Consequently, it would receive a stronger shock if the organ were insulated, with the exception of the particular column under consideration. This is represented in the figure, to the right of the sagittal plane, where the shading is intended to signify insulation. Thus, the current threads issuing from the margins of the dorsal surface and the upper half of the lateral surface of the column, can no longer pass through the adjoining columns to the corresponding points below the median transverse plane (which will be almost bent here to a

median transverse surface), but are compelled to go round by the edges of the organ. They have therefore to overcome an unequally greater resistance, and in the same proportion, constitute worse channels of collateral closure, which consequently have less power of weakening the currents which reach the little fish. Thus the insulating character of the organ would tend to increase the action of a conducting and electromotively active column on any part of the external space. The observation that in consequence of the insulating character of the organ the density of the currents flowing round it from the column is increased leads to the same result. This is seen on the right side of the figure, if regard is had to the limitation of the median transverse surface which presents itself as a consequence of insulation.

The only condition for the legitimacy of these conclusions is, that the resistance of the column should not disappear in comparison with that of external space. This condition in the case of the Torpedo is all the more certainly fulfilled, because, as we saw, the organ even at its best, conducts decidedly worse than sea-water.

Now the organ is not indeed insulated, but the irreciprocal conduction which we have recognised, performs, as has been already stated, a function similar to complete insulation. The current threads, with the deviation of which into badly conducting channels we are concerned, are all predominantly heterodromous where they meet the organ. Thus they encounter in the organ, a resistance which practically produces the same effect as if the organ were insulated. Each column conducts its own homodromous current comparatively well, but bars the passage to the heterodromous current threads of all the other columns ; and as this is the same for all the columns, the heterodromous current threads are forced to take the circuitous route round the edges of the organ, just as if the organ consisted of a non-conducting substance; and this remarkable behaviour is the result of irreciprocal conduction. The current of all the columns, and therefore the total current of the organ, increases in density in external space, that is, in physiological effect.

The increased strength of the shock produced thereby, is at all events more considerable, than that which would have resulted from the insulating property of the fascia covering the organ laterally, which the older investigators imagined to exist, for this would have cut off only the currents between points of the lateral

surfaces of the marginal columns, but would not have disturbed the heterodromous current threads in their course through the organ itself. The arrangement which does really exist, is superior even to the insulating property of the cover of the individual columns, for such a property would indeed oblige the currents, between points of the lateral surfaces of all the columns, to take their route along the column, but it would present no obstacle, to the return of the currents from the dorsal to the ventral surface, by the shortest route through the neighbouring columns. On account of the tenuity of the connective tissue sheaths of the columns, the proportion of the flow which equalizes itself through them, instead of through the external conducting mass, need not be taken into account, any more than that which follows the course of nerves and blood-vessels. The irreciprocity of conduction must be specially advantageous to the lower marginal columns of the organ, the proper homodromous current of which would otherwise be annihilated by the united heterodromous current threads derived from the median columns, which are about two-thirds higher and proportionally stronger.

It deserves to be remarked, that on the assumption that the shock is due to the marshalling of dipolar electromotive molecules in the electrical plate, all that has been said about the whole column may be equally applied to the individual molecule. Considering that the transverse section of the course of the homodromous current in the molecule is infinitely small, the resistance, notwithstanding the shortness of this course, is sufficient to justify the application of the above conclusions to the molecule also.

I endeavoured to give in the first communication an idea of the configuration, in a transverse plane dividing the organs about in half, of the system of current curves surrounding both organs; it is now necessary to alter this in consequence of irreciprocity of conduction, but I do not venture to say anything more decidedly about it. One thing alone is certain: the part of the animal which lies between the medial edges of the two organs, viz. its central nervous system, is, as was stated, in the course of the strongest flow; it will be traversed by even denser current curves than was before supposed. The immunity of the Torpedo in regard to electrical shocks (p. 432, 433), now an established fact, makes the difference unimportant.

What has been said here of the Torpedo, applies also essentially to the Gymnotus and the Malapterurus. It was in studying the

Malapterurus, that I first recognised the irreciprocal conduction, and traces of it are not wanting in Dr. Sachs' experiments on the Gymnotus. In these animals also, the impenetrability of the organ to heterodromous currents will tell in the same way in strengthening its action on external points. This will however be of special service to the Torpedo, for this fish is at a disadvantage, as compared with electrical fresh-water fishes, in consequence of sea water being so good a conductor.

I have on former occasions brought under notice, in electrical fishes, surprising instances of that organic adaptedness, which is ever a new source of wonder even to the strict adherent of mechanical causality. I showed how the construction of the electrical organ of the Torpedo on the one hand, of the Gymnotus and the Malapterurus on the other, is adapted to the different conducting power of sea and fresh water[1]; how with their growth, the organs of the Gymnotus and of the Torpedo change precisely in the way in which fresh and sea water demand[2]; how also the electromotive forces of both fish, according to all measurement, are in the same ratio to each other as the resistances of fresh and sea water[3]; how the circumstance that the organ is positively polarised by shocks of extremely short duration, tends to strengthen the shock, and how in consequence of the negative polarisability of the organ when tetanised, it is brought about that a fresh discharge starts again almost from zero[4]. I showed also the indispensable immunity of electrical fishes and their progeny in regard to electrical shocks. Finally, the remarkable mode of terminal branching, described by Wagner in the organ of the Torpedo, seems to be adapted to ensure the simultaneous coming into action of all electrical plates, innervated by the same primitive-nerve fibres[5]. But in one point only we failed to understand the arrangement of the Torpedo organ: it seemed to us, that the region which is above the back of the animal, in the neighbourhood of the sagittal plane, was, to borrow an expression from fortification, a dead angle, although it is precisely most in need of protection (434, 435). Now this drawback is undoubtedly to a certain extent remedied by irreciprocal conduction.

[1] Gesammelte Abhandlungen, vol. ii. p. 696.
[2] Untersuchungen, &c., p. 14 f.; Archiv für Physiologie, 1883, p. 252.
[3] Untersuchungen, &c., p. 411 f.
[4] Untersuchungen, &c., p. 220.
[5] Untersuchungen, &c., p. 293.

However that may be, the instance of internal adaptation to which we have been now led, far surpasses all earlier ones in ingenuity. It would certainly have demanded the profoundest reflection of a clever brain, to hit upon the idea of making each column as good a conductor for its own shock as any other animal tissue can be, but comparatively a non-conductor for the current of all other columns. In connexion with the extremely transitory nature of the shock, it is not a little remarkable, that it is only currents of extremely short duration that the organ conducts irreciprocally. Of what service would it have been to the fish, if it had become a perfect non-conductor for continuous heterodromous currents also[1]?

15. Positive polarisation in its dependence upon the density of the polarising current. A case of relatively positive polarisation by the heterodromous current.

By the establishment of irreciprocal conduction, a foundation hitherto wanting, has been gained for the investigation of the phenomena of polarisation in the electrical organ, in one direction at least. We no longer require to attribute a clearly quite inconceivable strength to the relatively positive polarisation produced by the homodromous current, nor an equally unaccountable transitoriness in the first moments after opening the polarising circuit, which is entirely at variance with its later persistence. From the circumstance that when the period of closure is lengthened, the homodromous current is stronger than the heterodromous, we cannot draw the conclusion which we held to be good in the first communication (p. 456), on the assumption that there is no such thing as irreciprocal conduction. Such conduction does exist, consequently that superiority may be the result of it; and as a further consequence, it does not prove that positive polarisation and the shock are different processes.

[1] It should be remembered, in regard to the history of the subject, that irreciprocal conduction has been brought into connexion with the shock of electrical fishes once before in a remarkable way. P. Erman's unipolar conductors, flame, soap, white of egg, and other animal substances, in a certain degree of dryness presented the earliest known instance of irreciprocal conduction. 'Noch frage man mich nicht,' he says in his somewhat curious language, 'ob ich wohl am Ende zu glauben vermag dass die erwähnte isolirende Eigenschaft der unipolaren Leiter . . . mit dem Mechanismus der Spontaneität der vorzugsweise sogenannten elektrischen Thiere einen denkbaren Zusammenhang habe. Ich kann diese Frage zur Zeit nicht beantworten, aber gestehen will ich dass ihrer Lösung mein Augenmerk bei dieser Untersuchung war.' Gilbert's Annalen der Physik, 1806, vol. xxii. pp. 44, 45.

The foremost duty enjoined seemed to be to establish more completely the dependence of absolutely positive polarisation upon the current density, but at the close of the first communication, I still needed systematic experiments on this subject. I have now made such experiments in such a manner, that I sent a momentary current of always the same duration through the same preparation, but the current was produced by a Grove's battery with a number of cells increasing from I. up to L. and decreasing again to I. The following numbers give a picture of the results:—

I.

4. Torp. Fresh. $OC + 0.0102$. $1' - P$.

CT 0″·0764.

	I.	V.	X.	XX.	XXX.	L.	XXX.	XX.	X.	V.	I.
S.	$+500+x$	$500+x$	250	250	—	315	125	41	10	−3	0
P.	3·5	20	38	87	148	322	152	78	35	18	2·5

	XX.	XXX.	L.
S.	+60	+43	+173
P.	78	173	319.

The preparation was very vigorous as the strong organ current shows; it shocks perceptibly the two first times, when excited by a current of only one Grove, and shows from thenceforward absolutely and relatively positive polarisation rising and falling regularly with the current density. A disturbance occurred with thirty cells, but it did not detract otherwise from the usefulness of the whole series.

II.

All as in Series I, except $OC + 0.0341$.

	I.	V.	X.	XX.	XXX.	I.	X.
S.	+3; +3	−5; −3 / +19; +10	−13 / +22	−7 / −	−13 / +9	−17 / +15 ↑ +238	−12
P.	3·5 ↓ 2·5	↓ 15·5; 15	32	64	97	178 267	↓ 34

I have given the second series, chiefly because it presents the example of absolutely negative, relatively positive polarisation by the heterodromous current; this is the instance mentioned above on p. 503, and though apparently incontestable, it is hitherto unique. The occurrence of this polarisation is all the more significant, as a relatively negative preliminary deflection precedes the relatively positive principal deflection. Thence we may infer, that the relatively positive heterodromous polarisation is always present, and is only concealed by the homodromous, relatively negative polarisation.

The first series shows in a very pronounced way, the phenomena which were described in general language in the first communication. It appears to support the assumption of an absolutely and

relatively positive polarisation, different from the shock and due to the homodromous current. A completely reliable proof of the correctness of the one or the other conception is wanting, such as would be afforded by a more frequent recurrence of the behaviour exhibited in the second series, as a set-off for the failure in obtaining the result sought after in § 6.

16. On conduction in both directions in the electrical nerves of the Torpedo.

In the experiments of the first communication, one question among others remained unanswered, which has indeed been decided long ago, but can never be too frequently made the object of renewed examination, viz. the question as to conduction in both directions (*doppelsinnige Leitung*) in the electrical nerves, the purely centrifugal character of which gives them inestimable value for this purpose. The first experiment which I made on the first fish (the one in a condition of opisthotonus) last summer, was aimed at this question.

With 10,000 turns at zero, the feeble current of the electrical nerves could be observed very well: the stronger negativity of the peripheral transverse section, upon which stress was laid in the first communication, could always be clearly made out. Thus I obtained for the nerves of the first Torpedo, which was unhealthy, the following values in Raoults :—

		I (left).	II.	I (right).
With peripheral...	Transverse section...	+ 0·00718	+ 0·00822	+ 0·00568
With central.....		− 0·00508	− 0·00568	− 0·00409
Difference.....		+ 0·00209	+ 0·00254	+ 0·00159

These numbers are in complete conformity with those in the first communication. On a later occasion, I tried to prove also that the electromotive force of the current ascending between two transverse sections of the electrical nerves—it may be called the axial current—increases in proportion to the length of the portion of nerve, but I did not succeed in this with the uniformity I could have wished. In observing the axial current between points in the longitudinal section of the uninjured nerve, which I also attempted (comp. p. 465), I met with the difficulty, that since the electrical lobes had been punched out, the negativity of the upper transverse section chiefly asserted itself. It will be

necessary to make the experiment on a Torpedo not divested of its electrical lobes, but it will then be difficult to prevent disturbances arising from voluntary or reflex shocks[1].

I now tetanised the nerves of the first Torpedo, from which the numbers given above were obtained on this occasion, with Helmholtz' arrangement of the sliding inductorium. The primary coil was filled with rods, and the shocks were led into the nerve by the clay points of the unpolarisable tubes. It was necessary to bring the secondary coil up to 30 mm. in order to obtain a good variation to the amount of 7–10 sc. The variation was observed repeatedly in the same nerve, with descending as well as with ascending direction of excitation, and thus this important gap has been filled up.

The disturbances which had shown themselves in the corresponding experiments of the first communication, now only occurred once. Ewald Hering recently made similar observations on the sciatic nerve of the frog[2], so that the fact has nothing whatever to do with the function of electrical nerves. It is attributable to the circumstance, that by the new methods, many minute details can now be recognised in phenomena which were formerly only sketched in outline. When the nerve was replaced by a clay model, there was no such effect on tetanising.

The next step was to observe electrotonus in the electrical nerves of the same fish. The experiments were conducted precisely as on the first occasion (p. 466). I also now saw anelectrotonic and kathelectrotonic increments spread in both directions, as Prof. Christiani had already done, but I had neglected this observation the first time, because my attention was taken up with disturbances which had hitherto been unexplained, and which presented themselves to me, as previously to Prof. Christiani. They were now also again noticeable. Electrotonic increments presented themselves in the wrong direction; after cutting through the nerve, there remained actions in the right direction and in considerable strength. The significance of these irregularities must be decided by further experiment.

[1] Very shortly, a paper worked out in the physical department of the Physiological Institute by Dr. M. Mendelssohn will appear in the Archiv für Physiologie; the axial current is here traced in different nerves acting wholly centrifugally or centripetally.

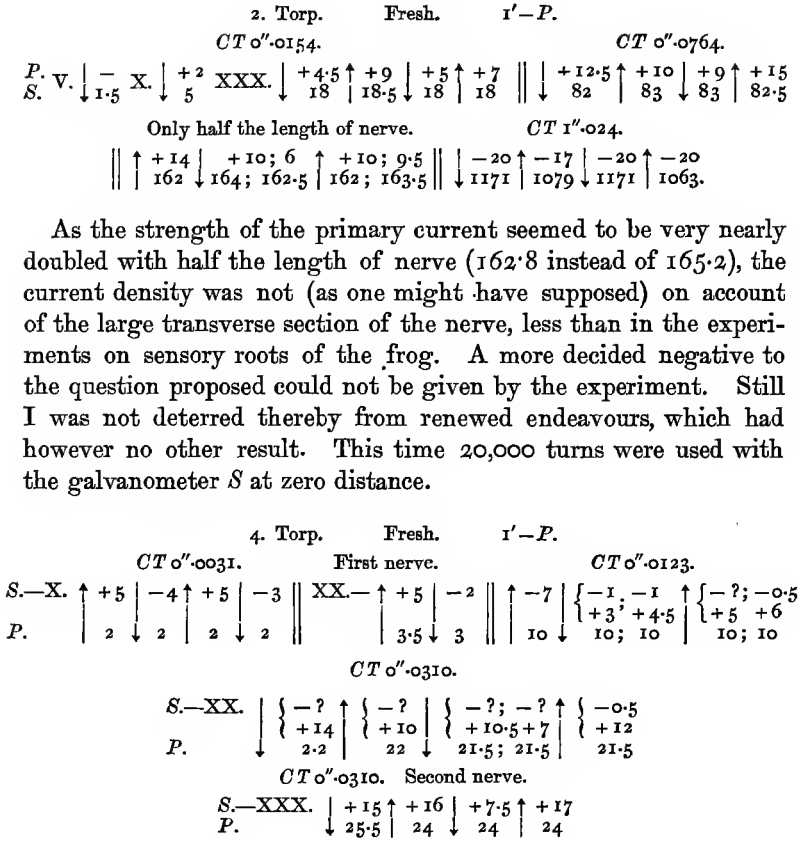
[2] Beiträge zur allgemeinen Nerven- und Muskelphysiologie, 15 Mittheilung. Über positive Nachschwankung des Nervenstromes nach elektrischer Reizung. In den Wiener Sitzungsberichte, 1884, vol. lxxxix. p. 137 f.

17. On the secondary electromotive phenomena in the electrical nerves of the Torpedo.

I endeavoured to answer the question as to the secondary electromotive behaviour of the electrical nerves in the second fish. It will be remembered that in the paper on the secondary electromotive phenomena of muscles and nerves, it is stated that positive polarisation by the ascending current, exceeds very uniformly that due to the descending current in the posterior roots of the spinal nerves of the frog. If here also we denote the physiological direction of action of the roots as homodromous, and the opposite as heterodromous, then positive polarisation in the homodromous direction is stronger than in the heterodromous. On the other hand, the corresponding difference in the case of the anterior roots is not so clear, and if at first it is seen, it is soon effaced; i.e. positive polarisation in the homodromous, here the descending direction, does not exceed perceptibly or not permanently that in the heterodromous, here the ascending direction[1]. On account of the great difficulty which attends these experiments on the roots, owing to their shortness and delicacy, it appeared extremely desirable to repeat these experiments on the electrical nerves, which, according to general opinion, can be obtained almost or wholly centrifugal, and of a length and thickness, such as is not to be met with in the animals which have hitherto been available for physiological experiment. I stated in the first communication (p. 463) that they can be easily found unbranched of a length of 3–4 cm., but I have since had them as long as 5·5 cm. with a thickness of 2·5 mm.

The nerves were laid in a groove, which was cut with a three-cornered file in a piece of cork afterwards varnished. The clay shields of the leading-in pads of the battery circuit were put upon the two transverse sections. The clay points of the unpolarisable tube electrodes, as terminals of the galvanometer circuit, were placed on symmetrical points of longitudinal section near both transverse sections. With this arrangement, the axial current made itself uniformly perceptible with a force of 0·00125 to 0·00212, corresponding as closely as possible to the difference recorded on p. 537. The galvanometer S had 10,000 turns at zero distance, and the galvanometer P 50 turns at 20 mm. distance. I obtained the following numbers:—

[1] Gesammelte Abhandlungen, 1883, vol. i. pp. 382–387.



As the strength of the primary current seemed to be very nearly doubled with half the length of nerve (162·8 instead of 165·2), the current density was not (as one might have supposed) on account of the large transverse section of the nerve, less than in the experiments on sensory roots of the frog. A more decided negative to the question proposed could not be given by the experiment. Still I was not deterred thereby from renewed endeavours, which had however no other result. This time 20,000 turns were used with the galvanometer *S* at zero distance.

After completing this series of experiments, it was discovered that in one place of the battery current, the conduction was imperfect; it was the same fault which had caused the derangement recorded above (p. 536). Still it does not seem that this would tend to diminish the significance of the negative result obtained, nor when we consider the variety of combinations of current densities and times of closing which were tried, is it to be expected that any later result will make any change in the conclusion now arrived at. We should however do wrong to rest perfectly satisfied, until the examination has been extended to other nerves of which the constituent fibres are physiologically homogeneous.

ADDENDUM.

During the period which has been occupied in preparing the foregoing Memoirs for the press, the nature of the secondary electromotive changes of nerve and muscle has continued to occupy the attention of physiologists. In order to render this series of memoirs more representative than it would otherwise be of the actual state of knowledge, without delaying its publication, it seems desirable to give a short account of one or two experimental researches which have very recently appeared relating to a subject dealt with in these memoirs.

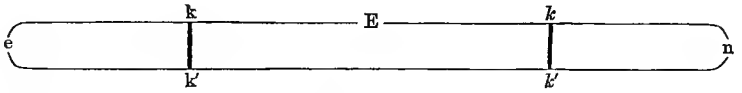
1. Intrapolar Polarisation of Nerve.

One of the questions to which the investigations of du Bois-Reymond, Hering and Hermann, have given special interest is that of the changes which take place in a nerve *during* the transmission through it of a voltaic current in the tract which intervenes between anode and cathode. Can it be demonstrated that an electromotive force which did not before exist, comes into existence in either direction in the intrapolar tract and, if so, what is its relation to the intrapolar after effects observed in the various modifications of Peltier's experiment?

The direct investigation of the intrapolar tract during the passage of a current is beset with difficulties, of which the most fundamental is that of discriminating between the galvanometric results of change of resistance and those of change of electromotive force. The first observations of any importance bearing on this subject were those of Professor Hermann, made some years ago, who found that when compared with the resistance of a living nerve, that of the same nerve when devitalised was considerably greater. Prof. v. Fleischl has recently attempted to get over the difficulties with the aid of the capillary electrometer[1]. He found that when he introduced a capillary electrometer into the

[1] E. v. Fleischl, Studien über den Electrotonus, 'Arch. f. Anat. u. Physiol.' 1885, p. 490.

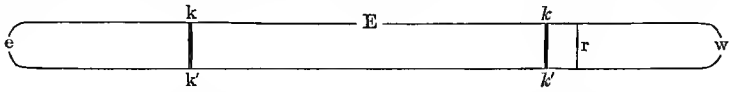
circuit of a thermopile, which circuit also included a 'currentless' nerve (i. e. a nerve to which the leading off electrodes were applied at equipotential points) the hydrostatic pressure required to zero the electrometer, i. e. to bring back the column of mercury to the position which it occupied when 'short circuited,' accurately indicated the electromotive force of the pile. In other words, it made no difference as regards the reading of the electrometer whether the polarised nerve were in or out of the circuit. The form of Fleischl's experiment, of which the result is regarded by him as inconsistent with all that has been advanced on the subject of nerve-polarisation on either side, may be described as follows:



The line e k E *k* n *k'* k' represents a circuit in which are included at n a nerve (by equipotential contacts) and at e a capillary electrometer, furnished with an arrangement by which the pressure of mercury in the capillary can be regulated and measured. k k' and *k k'* represent keys or bridges by which either nerve or electrometer can be short-circuited at will. At E an electromotive source is introduced into the circuit, which, as above stated, was in Professor Fleischl's experiments a thermopile, of which one set of junctions was heated by a small Bunsen. The experiment consisted in first measuring the electromotive force of E with *k k'* closed and k k' open, then closing k k' and opening *k k'* so as to lead the current of E through the nerve, and finally opening k k' so as to obtain a second measurement. It was found that the two measurements were identical. It was therefore evident that in the intrapolar tract, the effect of the polarisation of the nerve was not such as to balance the opposed polarisation of the electrometer. When the experiment was varied by substituting for the nerve a non-living polarisable arrangement—a voltameter of the kind known as 'Wollaston's points' (platinum wires fused into glass tubes so as to cover all but their tips)—the polarisation of the points evidenced itself by a diminution of the reading of the electrometer which persisted for some hours.

It is evident therefore that the polarisation of a nerve is not quite the same as the polarisation of a voltameter. As to what the difference consists in, Hermann has sought to enlighten us

in a very recent paper which purports to be a theoretical and experimental criticism of Fleischl's work [1]. A polarised nerve, he says, is not comparable to a voltameter, because in nerve, the polarised surface is not in the unbranched circuit but in a collateral branch (*Zweigkreise*), and that consequently the case of the nerve is not strictly represented by substituting for it the Wollaston's points at w in the diagram, unless at the same time a permanent derivation is introduced as under, in which r



represents a second bridge which in the experiment remains closed when k k′ is opened, and of which the resistance though considerable in itself, is small as compared either with that of w or with that of the unbranched part of the circuit. The reason why a current in passing along a nerve is divided into two channels is to be found, according to Hermann, in the fact that every nerve fibre consists of an axial core and of an envelope of different material, and that, whereas the latter conducts without polarisation, whatever proportion of the current enters the core from the envelope and then leaves the core to reenter the envelope, produces polarisation as it passes from the one to the other and *vice versâ*. The grounds on which Professor Hermann regards a nerve, so long as it is alive, as a conductor of this kind are so well known that it is scarcely needful to refer to them here. It will be sufficient to remind the reader that the electrotonic currents of nerve are reproduced or imitated in a model (*Drahtmodell* or *Kernleiter*) which, in accordance with the principle above referred to, consists of a core of wire sheathed in a moist envelope. When in Fleischl's experiment a model of this kind is substituted for the nerve at n (in the first diagram) it is found to behave exactly as a living nerve does. The introduction of the polarised model into the circuit is without influence as regards the reading of the electrometer, i. e. as regards the electromotive force indicated by it. The difference, therefore, between the negative polarisation of a nerve and that of any such polarisable arrangement as a voltameter is that whereas the nerve loses its charge in an open

[1] Hermann, Ueber die Ursache des Electrotonus, Pflüger's 'Archiv,' vol. xxxviii. p. 153.

circuit very rapidly indeed (according to Hermann by derivation (*Abgleichung*) through the envelope) the latter retains its charge under the same conditions for a considerable time. That this is actually the case, Hermann has shown by a separate series of experiments, in which he investigated with the galvanometer the state of polarisation of various polarisable arrangements (voltameter, Wollaston's points, wire model and living nerve) at various periods after the opening of a polarising current led through them, the result being that the nerve and wire model contrasted with the others in respect of the rapidity of their depolarisation.

In the introduction to his paper the subject is treated mathematically: it is shown that on the hypothesis that a living nerve possesses as regards polarisation the properties of the '*Kernleiter*,' the result of Fleischl's experiment must be as it actually is [1].

If the '*Kernleiter*' theory could be accepted as proved, the explanation might be regarded as satisfactory. But for the present a serious difficulty exists, in the fact that the extrapolar currents which are regarded as the characteristic phenomena of 'electrotonus' in the sense in which the word was first used by du Bois-Reymond, do not, as they ought to do if they are directly dependent on physical polarisation between the sheath and core of the nerve fibres, appear at the instant that the polarising current is closed. Not long ago an experiment was made by Helmholtz for the purpose of proving this [2]. It consisted in comparing the time which elapses when an excitatory wave is propagated through two nerve channels, of which one is an undivided nerve, the other consists of two nerves *a* and *b* of which the ends are opposed to each other in such a way that when a current of short duration is led through *a* where it is not in contact with *b*, *b* is excited by the electrotonus induced in the applied part of *a*. It being found that if the whole length of the channel of conduction was the same, the time lost in transmission was the same, it was concluded by Helmholtz that the rate of propagation of electrotonus did not materially differ from that of excitation. It has now been, so far as can be seen, conclusively proved by a new series of experiments conducted by Prof. Bernstein [3] with his repeating rheotome, that the electrotonic effect

[1] The answer which is expected from Prof. Fleischl has not yet appeared. Editor, April, 1887.

[2] Helmholtz, 'Monatsberichte der Berl. Acad.' 15 Juli, 1885.

[3] J. Bernstein, Ueber das Entstehen u. Verschwinden der electrotonischen Ströme im Nerven, 'Archiv. f. Anat. u. Physiol.' 1886, p. 197.

is propagated from cathode or anode as the case may be, at a rate of from 10 to 15 metres per second. As explanatory of the result of his very extended series of experiments, he gives the following diagram.

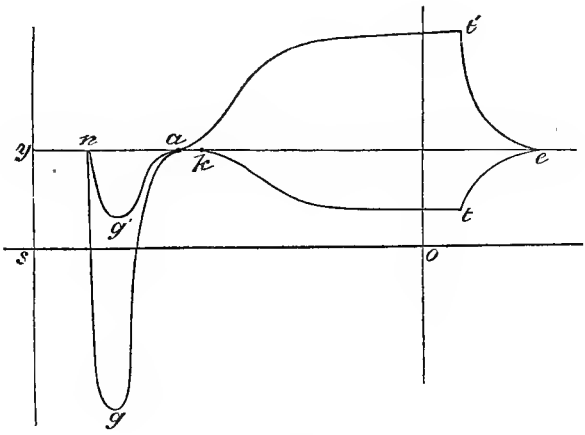


Fig. 24.

In the diagram, *S O* on the time axis expresses the duration of the closure of the polarising current, which in most of the experiments was about $\frac{5}{100}''$. When the distance between the intrapolar tract and the leading off electrodes (which were applied respectively to the natural and end surfaces of the nerve) was about 15 millims. the electrotonic effect began between $\frac{1}{100}''$ and $\frac{2}{100}''$ after the closure of the polarising current, the interval of time being always approximately proportional to the distance. When the current was so directed that the cathode was next the leading off electrodes, the excitatory wave due to the excitation at the cathode was strong enough to reverse the previous negativity of the end surface of the nerve, as shown in the diagram, where the difference of potential between the two leading off contacts is indicated by the distance *S y*, and the excitatory variation by the loop *n g a*. The cathelectrotonic effect which is of course in the same direction as the variation, does not begin until the latter has entirely ceased, as indicated by the line *k t e*. When the anode was next the leading off electrodes, there was also a feeble excitatory effect due to the same cause as before, but in this case its sign was opposed to that of the relatively much stronger anelectrotonic current *a t' e*. In both

cases the electrotonus ceased abruptly about $\frac{1}{200}''$ after the polarising current was broken.

Prof. Bernstein carefully avoids drawing any theoretical conclusions from his experiments, which must be regarded as a continuation of those embodied in his well-known 'Researches on the excitatory process in Muscle and Nerve,' published in 1871. He regards extrapolar electrotonic currents as indications of a 'state of polarisation peculiar to living nerve, which is propagated in nerve fibre from section to section,' but declines to express any opinion as to its relation to ordinary physical polarisation.

2. Time-relations of the excitatory process in Muscle and Nerve.

An investigation recently conducted in Prof. Hering's laboratory by Mr. Head of Cambridge[1] is of sufficient novelty in relation to the excitatory process in nerve to make it desirable that the reader should be informed on the subject.

Our knowledge of the time-relations of the process have been hitherto exclusively founded on the experiments of Bernstein with the repeating rheotome, recorded in his well-known monograph 'On the excitatory process in Muscle and Nerve.' Mr. Head's experiments on the subject have been made with an improved form of instrument, the construction of which renders it possible to subject a nerve to excitations of a frequency much greater than was attainable with the original rheotome of Bernstein, and thereby, as well as by employing a galvanometer better adapted to the purpose, to obtain indications of much greater delicacy than those afforded by Bernstein's method. As regards the duration of the negative variation, due to a single excitation, the new determinations show that Bernstein's estimate, which has up to the present moment been universally accepted, is very much too short, that the period of negativity lasts, even in the nerves of summer frogs, for more than a hundredth of a second, and in winter frogs twice as long. But this point, however interesting and important, was not the main object of the enquiry. Mr. Head's efforts were chiefly directed to obtaining determinations of the conditions which lead to the positive after effect which, as Hering showed in his paper 'On tetanic excitation of Nerve,' succeeds the concomitant diminution

[1] Henry Head, Ueber die negativen u. positiven Schwankungen des Nervensystems. Pflüger's 'Archiv,' vol. 40. p. 207, 1887.

or reversal of the 'demarcation current' at the moment that the excitation ceases. The main facts ascertained by Hering were that effects appeared even when the tetanisation lasted only a fragment of a second, and that when the excitation was prolonged in successive experiments, the positive after effect increased up to a duration of 30″, but subsequently diminished.

To these facts Mr. Head has added the following. He has first shown that the positive after effect cannot be regarded as a second phase of the excitatory effect produced by each single excitation, for his rheotome observations show that the negative phase is followed by a period of complete restoration of the previously existing electrical state, which lasts for several hundredths of a second. Secondly, he has shown that in short tetanisation lasting not more than a few seconds, the excitatory effect, i. e. diminution of the demarcation current, is nearly constant—a result which could not happen unless the positive effect were deferred. Thirdly, that in comparing nerves prepared with the utmost possible care and protected from evaporation, with nerves in a less favourable state, it is found that although the latter may show no inferiority or sign of impaired functional activity as regards the negative variation, they are inferior as regards the positive after effect, so that, in repeated observations, the former remains unimpaired while the latter rapidly diminishes.

These facts he interprets to mean that the positive after effect is in the nature of a reaction of the nerve, consequent on excitation, i. e. a change in the opposite direction to the excitatory change, by which it not merely returns to the normal, but passes into a condition on the other side of the normal, so that the longitudinal surface to which the electrode is applied becomes more positive than it was before excitation. This view he considers to be confirmed by the observation that the effect in question is only observed when the leading off contact on the longitudinal surface is at a considerable distance from the injured end of the nerve.

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